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Resource partitioning in a guild of marsh dwelling *Agonum* (Coleoptera: Carabidae)

by

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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W. G. Evans
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Mark V. H. Wilson

Date October 2, 1981

ABSTRACT

This study investigated the natural history of microsympatric species of *Agonum* (*Europhilus*) inhabiting eutrophic marshes in the George Lake area of central Alberta. The overall aim was to assess how adult populations were distributed in space and time and how niche differences among species may help account for their coexistence in single marshes. Habitat use, population dynamics and reproduction, daily activity, regional patterns of wing dimorphism and climbing behavior were compared among species. Niche partitioning is realized mainly through segregation over both macro- and microhabitats and in reproductive periods.

A. nigriceps, *A. ferruginosum*, *A. thoreyi* and *A. lutulentum* are the most abundant species in marshes of the study area. Their populations occupy the inundated zone of marshes. The restriction of most other carabids to the marsh unflooded edges suggests that inundation affects the spatial distribution of carabids within marshes.

A. nigriceps, *A. ferruginosum* and *A. lutulentum* are associated with single macrohabitats defined by vegetation type: *A. nigriceps* and *A. lutulentum* with sedge tussocks, *A. ferruginosum* with floating cattails. *A. thoreyi* is a macrohabitat generalist distributed across marsh zones.

At the microhabitat level, *A. ferruginosum*, *A. thoreyi* and *A. lutulentum* are markedly associated with dense patches of dead growth, dense tussocks and emergent substrate, suggesting that vegetation structure and emergent substrate affect the distribution of these species in the flooded zone. *A. nigriceps* is a microhabitat generalist.

Overwintered adult populations of *A. nigriceps*, *A. ferruginosum*, *A. thoreyi* and *A. lutulentum* are not separated seasonally. Reproduction begins at spring thaw for *A. nigriceps* and *A. ferruginosum*, but starts three to four weeks later for *A. thoreyi*, possibly leading to the segregation in time of hatching peaks of larvae. *A. nigriceps*, *A. ferruginosum* and *A. thoreyi* are nocturnal and are not separated in time on the daily scale.

The relative proportions of macropters and brachypters of *A. nigriceps* vary markedly from marsh to marsh, possibly owing to island-like effects of the regional mosaic of marshes. Populations of *A. ferruginosum* are virtually all macropterous in the study area.

Laboratory experiments show that adults of *A. nigriceps* have the highest propensity to climb on narrow vertical structures and this may explain association with structurally simple emergent vegetation. Climbing tendencies were generally higher for adults of species found in inundated vegetation than for those inhabiting the unflooded marsh edges. This may be an adaptation to increase foraging efficiency of the former on emergent vegetation. The high climbing propensity, short tibiae and long tarsi, and cryptic coloration of *A. nigriceps* specimens suggest that the species is best adapted to life on emergent vegetation of marshes.

High population densities of inundated marsh *Agonum* are possibly linked to use of the three-dimensional vegetation as a habitat. There is no relationship between niche breadth and abundance within the *Agonum* guild of flooded marshes. Niche breadth relative to spatial aspects of niche axes varies between marshes and is possibly a function of microsite distribution for *A. ferruginosum* and *A. thoreyi*. Niche overlap is highest between *A. ferruginosum* and *A. thoreyi*, which are best separated by a difference in onset of the reproductive period. *A. nigriceps* is mainly separated from both former species through habitat differences. *A. lutulentum* populates very few marshes of the study area, and a mutually exclusive macrohabitat distribution relative to *A. ferruginosum* suggests interspecific competition with this species in marshes where both are abundant.

Availability of suitable, structurally complex patches of vegetation in the inundated marsh zone may be a key variable regulating the distribution and abundance of *Agonum* species within marshes, with the sporadic occurrence of competition and the action of predators affecting population performances and producing the observed patterns of niche partitioning.

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Table of Contents

Chapter Page

ABSTRACT iv

ACKNOWLEDGEMENTS vii

TABLE OF CONTENTS x

LIST OF TABLES xv

LIST OF FIGURES xvii

1. INTRODUCTION 1

  1.1 The coexistence of species 1

    1.1.1 Niches, resource partitioning and coexistence 1

    1.1.2 Coexistence in carabid beetles 4

  1.2 Marsh dwelling *Agonum* 8

    1.2.1 The subgenus *Europhilus* and other closely related *Agonum* 8

    1.2.2 Natural history 9

    1.2.3 Geographical distribution 12

    1.2.4 The problem and the approach 12

  1.3 The study area 16

    1.3.1 Sites and marshes 16

    1.3.2 Climatic conditions 19

2. HABITAT AND MICROHABITAT USE 21

  2.1 Introduction 21

  2.2 Material and methods 23

    2.2.1 Macrohabitat and microhabitat recognition ...23

    2.2.2 Sampling method and abundance estimates 27

    2.2.3 Sampling programme 30

    2.2.4 Treatment of the data 32

2.3 Results 33

2.3.1 Composition of marsh carabid fauna 33

2.3.2 Species distribution in relation to inundated areas 35

2.3.3 Macrohabitats 35

2.3.4 Microhabitats 46

2.3.4.1 Dead growth patches 46

2.3.4.2 Emergent substrate 49

2.3.4.3 Sedge tussocks 49

2.4 Discussion 55

2.4.1 Inundation and species distribution 55

2.4.2 Species distribution and microclimatic factors 57

2.4.3 Vegetation structure, habitat segregation and coexistence 58

2.4.3.1 Vegetation structure 59

2.4.3.2 Competition 61

2.4.3.3 Density compensation 62

3. PHENOLOGY, DAILY ACTIVITY AND ALARY MORPHISM 64

3.1 Introduction 64

3.2 Material and methods 67

3.2.1 Seasonal abundance 67

3.2.2 Recognition of teneral adults 67

3.2.3 Condition of ovaries 67

3.2.4 Enclosure experiment for daily activity 68

3.2.5 Wing morphs of *A. nigriceps* and *A. ferruginosum* 72

3.3 Results 74

3.3.1 Adult population dynamics 74

3.3.2 Teneral emergence sites 82

3.3.3 Ovary condition and reproductive effort 82

3.3.4 Developmental time 90

3.3.5 Daily activity 90

3.3.6 Regional distribution of wing dimorphic *Agonum* 90

3.4 Discussion 98

3.4.1 Adult mortality 98

3.4.2 Timing differences and life history adaptations 99

3.4.3 Wing dimorphism and marsh colonization 103

3.4.3.1 Wing dimorphism in *A. nigriceps* 104

3.4.3.2 Wing dimorphism in *A. ferruginosum* .106

4. EXPERIMENTAL ANALYSIS OF CLIMBING BEHAVIOR 107

4.1 Introduction 107

4.2 Material and methods 109

4.2.1 Species tested and hypothesis 109

4.2.2 Apparatus and laboratory conditions 110

4.2.3 Experimental procedure 113

4.2.4 Treatment of the data 114

4.2.5 Morphometric data 114

4.3 Results 116

4.3.1 Species tendencies to climb 116

4.3.2 Leg size and climbing 125

4.4 Discussion 130

4.4.1 Habitat structure and climbing 130

4.4.2 Leg size and climbing 131

4.4.3 Climbing and crypsis in *A. nigriceps* 133

5. COMMUNITY ANALYSIS AND GUILD STRUCTURE 140
5.1 Introduction 140
5.2 Methods 142
5.2.1 Niche breadth 142
5.2.2 Niche overlap 142
5.2.3 Dendrograms 143
5.2.4 Spatial association analysis 144
5.2.5 Size relationships 145
5.3 Results 146
5.3.1 Macrohabitat relationships of the community 146
5.3.2 Niche breadth 153
5.3.3 Niche overlap 155
5.3.4 Spatial association 157
5.3.5 Size relationships 161
5.4 Discussion 165
5.4.1 Macrohabitat overlap and diversity 165
5.4.2 Breadth, overlap, and niche structure 169
5.4.3 Competition and size relationships 173
6. GENERAL DISCUSSION 177
6.1 Resource partitioning among adult carabid populations 177
6.2 Evolution and maintenance of niche differences ...182
6.3 Concluding remarks 186
LITERATURE CITED 188
APPENDIX I 200
APPENDIX II 202
APPENDIX III 205

APPENDIX IV 207

AUTOBIOGRAPHY 210

LIST OF TABLES

Table Page

1. Species of *Agonum* (*Europhilus*) known from the George Lake study area, Barrhead Co., Alberta 13

2. Marsh macrohabitat classes and their characteristic vegetation 24

3. Species of carabids sampled at the two main study sites in 1980, and their relative abundances 34

4. Percentages of teneral *Agonum* found in various macrohabitat categories of the two main study sites 83

5. Time relation between female egg production and teneral emergence in 1980 91

6. Distribution of wing morphs of *A. nigriceps* in various marshes 94

7. Chi-square values for test of independence of wing morphs of *A. nigriceps* with respect to sexes in various marshes 96

8. Two-way analyses of variance for the percentage of beetles climbed on sedge straws 124

9. Mean values of body and leg measurements and overall climbing scores for the species of *Agonum* tested in climbing experiment 3 126

10. Pearson's and partial correlation coefficients for morphometric data and climbing scores from climbing experiment 3 127

11. Average species densities in macrohabitat categories at the two main study sites 152

12. Niche breadth values and abundance rank of the dominant species of marsh *Agonum* with respect to three resource sets 154

13. Overlap values for three resource sets among the dominant species of marsh *Agonum* at George Lake site 156

14. Association indices (Kendall's Tau) between co-abundances of marsh *Agonum* species in samples from various macrohabitat classes 158

15. Body sizes and labrum widths of co-occurring adults of marsh *Agonum* 162

16. Body sizes and labrum width ratios for co-occurring adults of marsh *Agonum* 164

17. Summary of the main natural history features of the four dominant species of marsh *Agonum* in the George Lake study area, Alberta 178

LIST OF FIGURES

Figure Page

1. Map of the George Lake area, showing study sites 17

2. Cross-section outline of macrohabitat zones of a typical marsh of the study area 25

3. Relative abundance of carabid species in flooded and unflooded marsh zones at the George Lake study site 36

4. Relative abundance of carabid species in flooded and unflooded marsh zones at the Barrhead study site 38

5. Densities of species of *Agonum* in various marsh macrohabitats at the George Lake study site 41

6. Densities of species of *Agonum* in various marsh macrohabitats at the Barrhead study site 43

7. Distribution of species of *Agonum* in relation to patches of dead growth in sedge meadow and in cattails 47

8. Distribution of species of *Agonum* in relation to emergent substrate in cattails 50

9. Distribution of species of *Agonum* with respect to type of sedge tussocks 53

10. Field enclosure used to study daily activity 70

11. Overwintered and teneral adult population curves for species of marsh *Agonum* at George Lake during 1980 75

12. Overwintered and teneral adult population curves for species of marsh *Agonum* at Barrhead during 1980 77

13. Abundance curves for teneral adults for species of marsh *Agonum* during 1980 80

14. Seasonal distribution of ovary conditions in females of marsh *Agonum* species during 1980 84

15. Seasonal distribution of reproductive effort of marsh *Agonum* species during 1980 88

16. Daily locomotory activity of species of marsh *Agonum* in an experimental field enclosure 92

17. A beaker with mud substrate and sedge straws used for climbing experiment 111

18. Climbing frequencies of *Agonum* species in experiment 1 (1978) 117

19. Climbing frequencies of *Agonum* species in experiment 2 (1979) 119

20. Climbing frequencies of *Agonum* species in experiment 3 (1980) 121

21. Typical resting posture of *A. nigriceps* on a sedge leaf 134

22. Body outlines of *A. nigriceps* and of spiders found in the marsh vegetation 137

23. Dendrogram showing grouping by overlap values for macrohabitat of the marsh carabid community at the George Lake study site 147

24. Dendrogram showing grouping by overlap values for macrohabitat of the marsh carabid community at the Barrhead study site 149

25. Plots of pairwise numbers of individuals of the main species of *Agonum* found in the same samples 159

1. INTRODUCTION

1.1 The coexistence of species

1.1.1 Niches, resource partitioning and coexistence

Explaining organic diversity, its evolution and maintenance constitutes a formidable challenge to biologists and has brought them to investigate strategies whereby species live together in their environment. Such endeavors led early naturalists to formulate the idea of a niche for each species, this being understood either as a species' role or function in the environment (Elton, 1927: 63) or alternatively, as the ultimate fraction of a habitat occupied solely by one species (Grinnel, 1924).

The concept of niche, however, long remained a vague notion until Hutchinson (1957), in a seminal paper, gave it a formal expression as an abstract multidimensional hypervolume whose many dimensions represented species' fitness functions with respect to various biotic and abiotic factors. The so-called fundamental niche is the hypervolume physiologically and reproductively used by a species when it is alone in the environment, but this form is probably never realized in nature. The "actual" niche (Colwell and Futuyma, 1971), i.e. what is observed about a species in a community, is the hypervolume resulting from constraints at the populational level imposed by the available range of resources and by other members of the community.

Almost simultaneously with the formulation of his niche model, Hutchinson (1959) posed the question: "Why are there so many kinds of animals?", sparking a plethora of investigations that attempted to expose differences among sympatric species through which coexistence is achieved. Such studies of resource partitioning have focused on closely related species, usually congeners, for it is presumed that problems of coexistence should be more acute within these guilds owing to structural and behavioral similarities, an idea whose germ can be traced back to Darwin (1859: 59).

Through contemporary studies, representation of the Hutchinsonian niche axes gradually became identified with use patterns of resource spectra by species, in lieu of the ideal, but far less easily measurable fitness functions of the model (Pianka, 1976). The embodiment of ecological processes into the modern niche theory has led to the predominating view that coexistence is primarily a matter of minimizing or avoiding competition (Schoener, 1974). Niche differences and patterns of resource divisions are frequently thought to have evolved and be maintained through competitive interactions (MacArthur, 1972b; Cody and Diamond, 1975; Diamond, 1978). Nevertheless competition has remained adamantly elusive to demonstrate (Pianka, 1978: 244) and convincing evidence of its operation in nature, or lack thereof, through carefully designed experiments (e.g.

Connell, 1961; Wilbur, 1972) is as yet scarce (Wiens, 1977). Critical evaluations of current theory (Connell, 1975; Menge and Sutherland, 1976; Wiens, 1977) have pleaded for more investigations of the impact of other processes on coexistence, such as predation, density-dependent selection and environmental harshness, and for their incorporation into community models.

A great deal of the data basis used in elaborating resource partitioning and community structure theories was gleaned from studies of vertebrates, especially birds (MacArthur, 1972b; Cody, 1974; Diamond, 1975) and reptiles (Pianka, 1973, 1975). MacArthur (1972a) suggested that this state of affairs might be due to the conspicuousness of birds in the environment and perhaps also because birds appear "more tightly packed". Similar studies of insects (reviewed in Price, 1975) are comparatively few and have concentrated on parasitic groups, particularly Hymenoptera (Heatwole and Davis, 1965; Price, 1975: 298ff; Longair, 1978; Miller, 1980).

Yet insects must certainly have packed their environment since their unequalled diversity accounts for more than 80% of all animal life. Neglect of insects in studies of coexistence phenomena possibly stems in part from intrinsic difficulties in dealing with them (Spence, 1979a), especially from the fact that environmental changes occur on the same time scale as insect life cycles, therefore possibly preventing their populations from reaching equilibrium (Hutchinson, 1965: 61; Janzen, 1977). Insect niches may be expected to be enormously complex owing to interactions among resource dimensions and across trophic levels (May, 1973: 6).

Unravelling precise modes of resource partitioning is essential to an understanding of community organisation and ultimately, species diversity (Pianka, 1978: 244). But it is above all crucial to acquire a thorough knowledge of the details of natural history of the species under study (Hutchinson, 1975) if factors relevant to their coexistence are to emerge; the present study was undertaken in this spirit.

1.1.2 Coexistence in carabid beetles

Carabid beetles should be, at least in theory, ideal subjects for the study of coexistence problems: they are ubiquitous elements of the epigaeic fauna (at least in temperate regions), they are generally opportunistic predators-scavengers, and their larvae have voracious predatory habits and a strong propensity to cannibalism. Moreover, staggering assemblages of congeneric species live in structurally simple habitats (Andersen, 1969; Spence, 1979a). Despite these excellent opportunities and considering the relatively high degree of knowledge attained about this insect family (see Thiele, 1977, and Erwin *et al.*, 1979), works on resource partitioning in carabids remain scarce.

There are ample demonstrations that carabids are very sensitive to environmental features such as temperature, humidity and light, and that they exercise habitat selection (reviewed in Thiele, 1977; see also Andersen, 1978). The abundance of endeavors on habitat selection and its relationships to physiological demands and life cycles seems to have crystallized into the notion that carabid distribution and abundance are overwhelmingly regulated by these processes (Thiele, 1977: 209 and 312; 1979), and that the evolutionary success of carabids can be linked to their "many physiological adaptations to their habitats" (Thiele, 1977: 312). On the other hand, the importance of biotic factors is largely regarded as insignificant. The hiatus is that much of the data basis supporting such assertions comes from laboratory experiments testing isolated factors. These say little about responses of carabids in nature under oscillatory conditions (Spence, 1979a).

Albeit preferences recorded in the laboratory for species tested singly may corroborate field distributions, they only provide rough estimates of the fundamental niche relative to the variables measured, and do not yield information about how field distributions may be altered by the presence of other species and/or predators. Hutchinson (1978: 172) moreover pointed out the improbability of niches defined solely by physicochemical factors, because natural selection would continually operate toward a widening of tolerances. Recent arguments stressing the importance of environmental variability (Wiens, 1977) also argue against abiotic factors as being the sole significant regulators of carabid distribution and abundance.

Reasons underlying carabid coexistence may not be as simple as the ones currently advocated. Complex questions of interspecific interactions, predation and environmental heterogeneity still warrant more attention in the field. Specifically, more extensive and detailed field work on the natural history of co-living congeneric species is needed to provide a sound basis for detecting and testing coexistence mechanisms.

Many comparative studies of carabid natural histories have been of species occupying quite different habitats (e.g. Thiele, 1964; Paarmann, 1966; Barlow, 1970; Bauer, 1974) or of unrelated species in the same habitat (e.g. Mitchell, 1963), or still of so large assemblages of species from one habitat (e.g. Schjøtz-Christensen, 1965; Mossakowski, 1971) that little insight about coexistence mechanisms is gained. Not surprisingly too, evidence for interspecific interactions was not found in such studies. Yet if biotic factors such as competition affect carabid populations at all, they will be first suspected through careful examination of resource use and life histories of proximately coexisting species, and then through comparison of these same species in allopatry.

Studies that focused on co-occurring congeners (Gilbert, 1956; Dawson, 1965; Andersen, 1969; Carter, 1971) have yielded suggestive results, but have failed to examine these in light of modern ecological theories. In an inspiring paper, Spence (1979a) shows how carabidology and niche partitioning theory can mutually gain from interacting.

The overall purpose of the present study was to document the comparative natural histories of a group of sympatric carabid beetles of the genus *Agonum* (Coleoptera: Carabidae) inhabiting marshes in central Alberta, and to interpret the results in light of current theories. Problems of habitat occupancy and of phenology were especially addressed. The work is largely empirical, and thus constitutes only a first step in investigating distribution and abundance in relation to coexistence. Its results lay a basis for generating hypotheses about mechanisms of coexistence that could then be tested experimentally in future works. A more specific exposition of the problem is provided in the next section.

1.2 Marsh dwelling *Agonum*

1.2.1 The subgenus *Europhilus* and other closely related *Agonum*

The subgenus *Europhilus* is placed within the genus *Agonum*, a large assemblage of carabids distributed worldwide, though more diverse in the temperate regions and particularly abundant in the Nearctic region (Lindroth, 1966: 556). *Europhilus* forms a quite distinct taxonomic entity, on the basis of both adult and larval characteristics (Lindroth, 1955a, 1966: 570), and as such has already been treated as a separate genus (e.g. Casey, 1920: 125; Jeannel, 1942: 890). Current classifications (e.g. Lindroth, 1966) suggest that close relatives of *Europhilus* in the Nearctic region are the subgenera *Platynomicrus* and *Stictanchus*, respectively including *A. nigriceps* and *A. ferruginosum*. Larval characters of these two species suggest that they may be more closely related to *Europhilus* than is currently thought (pers. obs.). Because *A. nigriceps* and *A. ferruginosum* also share great similarity in general ecological requirements with several other members of *Europhilus*, I will herein, and for the purpose of this study only, treat them as if members of *Europhilus*.

1.2.2 Natural history

All Nearctic species of *Europhilus* but one (*A. retractum*, a forest dweller) are more or less markedly hygrophilous and live at the margin of standing waters, wet woodlands, or marshes with luxuriant vegetation (Ball, 1960; Lindroth, 1966: 570). Though some species appear to be somewhat restricted in habitat [e.g. *A. simile* at the margin of cold ponds with a carpet of moss (Lindroth, 1966: 571)], many are typically associated with eutrophic marshes and often co-occur in the same marsh. Some species (*A. thoreyi*, *A. lutulentum*, *A. nigriceps*, *A. palustre*) are known to occur among the emergent vegetation of marshes (Lindroth, 1955a, 1955b: 129, 1966: 579ff) and *A. galvestonicum* has been taken inside convoluted cattail leaf blades (Lindroth, 1966: 583). *A. nigriceps* females even oviposit exclusively on plants such as sedge and cattail (pers. obs.).

Previous studies of European *Europhilus* (Dawson, 1965; Murdoch, 1966a; Wasner, 1979) indicate that they are so-called spring breeders: adults reproduce in spring and larvae develop during the summer; tenerals emerge in late summer or in the fall and overwinter in reproductive diapause, along with surviving individuals of the parent generation. Both generations of adults may occur together throughout the year, though in varying proportions, and some individuals may reproduce twice over two spring seasons (Murdoch, 1966a, 1966b). Present evidence about overwintering (Larochelle *et al.*, 1976; Larochelle, 1978;

Garneau and Liard, 1979; and this study) suggests that the North American species are also spring breeders. Overwintering takes place in sites somewhat elevated from the surrounding marsh litter, such as logs, stumps, plant tussocks and heaps of dead grass, where risks of flood are smaller (Dawson, 1965; Murdoch, 1966a). Some individuals leave the marsh and overwinter in the humus-leaf litter or at the base of stumps of nearby forest (Larochelle, *et al.*, 1976; and pers. obs.).

Most *Europhilus* (*sensu* Lindroth) adults have fully developed wings [except the forest species *A. retractum*, which is polymorphic (Lindroth, 1966: 577; Carter, 1976)]. However in some species, the wings are so weakly veined that they seem unlikely to be functional (Lindroth, 1966: 571ff). *A. nigriceps* and *A. ferruginosum* are both truly wing dimorphic, some adults with fully developed wings, others with tiny stubs. Adults of *A. thoreyi*, *A. lutulentum*, *A. consimile*, *A. sordens*; *A. ferruginosum* (Lindroth, 1955a, 1966) and *A. nigriceps* (J.D. Fournier, pers. comm.) are all known to fly. Adults of the latter three species fly readily during sunny spring days (J.D. Fournier, pers. comm., and pers. obs.).

Little is known of the exact food habits of *Europhilus* species. *A. fuliginosum*, a European species, is principally a scavenger and probably a predator of slow moving animals (Dawson, 1965). Wasner (1979) reported that adults of four European species, including *A. thoreyi*, were omnivorous in the laboratory, even accepting plant material as food. Since the vast majority of carabids are predators-scavengers (Thiele, 1977: 107), it is likely that the North American members of *Europhilus* have natural food habits similar to those of their Palearctic congeners.

Parasites and predators of *Europhilus* and their effects on populations are inadequately known. Infestations by fungi (esp. Laboulbeniales) have been reported (Wasner, 1979), and were frequently seen in tallied or collected specimens during the course of this study, but it seems doubtful that they exert any detrimental effects on their carabid hosts (Thiele, 1977: 81). Mites were also often observed on adults of all species in the field, and extreme infestations (whole body covered) were seen in some laboratory confined animals. However the latter did not seem significantly affected in any way and it is likely that mites are merely phoretics or commensals. Nematode infestation was seen in only one female *A. thoreyi*, out of about 1200 individuals of *A. nigriceps*, *A. ferruginosum* and *A. thoreyi* that were dissected for various purposes during this study. Available evidence for predators suggests that shrews may significantly prey upon marsh *Agonum* (Murdoch, 1966a), although their actual impact on populations is not documented.

1.2.3 Geographical distribution

Europhilus is predominantly a northern group, both in the Palearctic and Nearctic regions (Lindroth, 1966: 571). The Nearctic fauna is particularly rich (Ball, 1960) with fourteen described species (Lindroth, 1966: 570ff, 1969: 1119). Most species are very wide ranging geographically: among the Nearctic members, seven are transamerican and three are Holarctic. Species richness peaks in eastern Canada-northeastern United States. *A. nigriceps* and *A. ferruginosum* are also northern in distribution, the former being more so and transamerican, the latter being exclusively western.

In the George Lake study area in central Alberta, ten species are known to occur (Table 1), eight of which are found at a single study site (Lake 1+2, see Figure 1). Available data (Lindroth 1966: 570ff and the University of Alberta Strickland Museum Collection) suggest that all species are well within their geographical ranges in the study area. Thus this assemblage of species shows a high degree of sympatry while at the same time presenting a relatively low ecological diversification. This raises interesting questions about coexistence in the group.

1.2.4 The problem and the approach

Murdoch (1966a) noted that marsh carabids afford appreciable advantages for study in that their populations are among the most dense recorded for Carabidae (this is

TABLE 1

Species of *Agonum* (*Europhilus*) known from the George Lake study area, Barrhead Co., Alberta

SPECIES	GENERAL DISTRIBUTION[1]	GENERAL HABITAT[1]
A. consimile Gyll.	subarctic and circumpolar	marshy ground with moss
A. picicornoides Lth.	transamerican[2] but somewhat local	moist grounds, often under brush canopy with leaf litter
A. sordens Kby.	transamerican	as *A. picicornoides*
A. retractum LeC.	transamerican	woodlands
A. gratiosum Mann.	transamerican	eurytopic, moist to wet places
A. superioris Lth.	transamerican	eutrophic marshes
A. thoreyi Dej.	Holarctic	eutrophic marshes
A. lutulentum LeC.	transamerican	eutrophic marshes
A. nigriceps LeC.	transamerican and Kamchatka Peninsula	eutrophic marshes
A. ferruginosum Dej.	western half of North America	eutrophic marshes

[1] Source: mainly Lindroth (1945, 1955a, 1955b, 1966: 570ff) and Larochelle (1975).

[2] Transamerican is here understood as encompassing only the northern half of North America (see text).

particularly true for *Agonum* species), and that they frequent well defined habitats in which emigration and immigration would be slight. This makes them attractive candidates for examining problems of species packing.

Dawson (1965) working on fenland carabids detected moderately distinct habitat associations among four species of marsh *Agonum*. She also found that overwintering sites were different from the summer ones, but that discrepancies in species habitat were maintained during hibernation. Some temporal separation was observed with respect to breeding and hibernating times, while food segregation appeared insignificant. Differences in timing of the breeding season were also noted by Wasner (1979) among microsympatric *Europhilus* of southwestern Germany. Murdoch (1966a, 1966b), working in England, suggested that population stability might revolve around patterns of survival in marsh *Agonum*, while Wasner (1979) observed discrepancies in species fecundity that could account for differential population success. These works suggest that a complex combination of subtle niche differences mainly involving temporal and spatial dimensions would allow population persistence and species coexistence among marsh *Europhilus*.

Hence the present study focused on the separation of species in space and time. Serious obstacles to the sampling of larvae forced the work to concentrate on adults. The three main aspects considered were:

(1) Habitats and microhabitats. Species distributions relative to marsh zones and microhabitat features were studied at two seemingly comparable marshes (Chapter 2) to evaluate extent of habitat partitioning.

(2) Population dynamics and reproduction. Adult populations of the dominant species were followed over the course of one summer, along with dynamic aspects of reproduction (Chapter 3) in order to assess possible time segregation. Wing dimorphism was also surveyed to explore how it may relate to marsh colonization from a regional perspective.

(3) Behavior. The tendency of species to climb was compared experimentally (Chapter 4) as a possible behavioral correlate of the occupation of flooded habitats.

Finally the data were analysed synthetically using some of the mathematical techniques of niche theory (Chapter 5), in an attempt to provide a condensed picture of resource partitioning among marsh guild members.

1.3 The study area

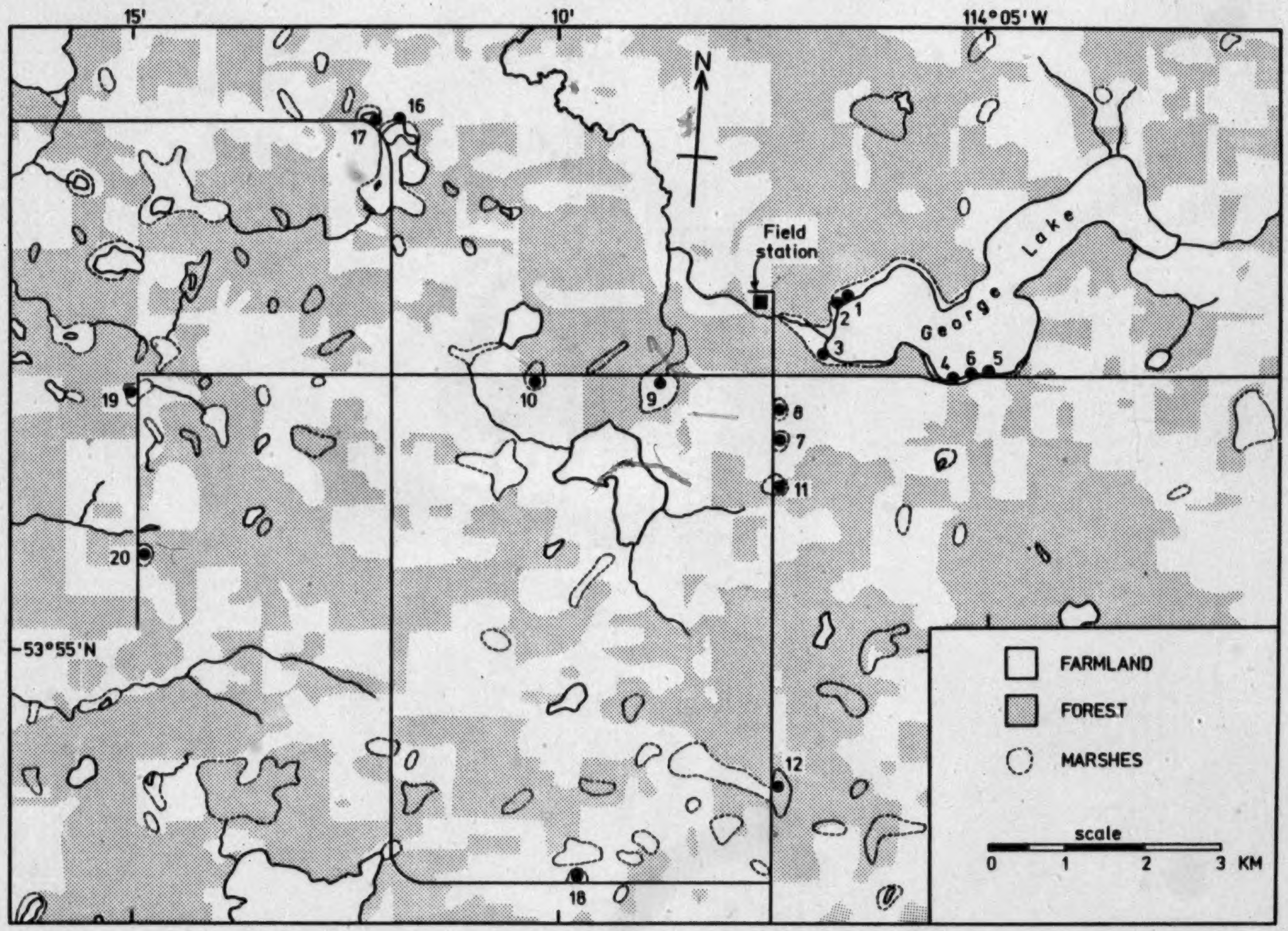
1.3.1 Sites and marshes

Field work reported in this thesis was conducted in the George Lake area, Barrhead Co., Alberta, about 40 miles northwest of Edmonton. Study sites are located in the area between 53°53′N – 53°59′N, and 114°03′W – 114°15′W, at elevations between 660 and 700 m. Pristine vegetation is that of the boreal forest-parkland transition zone (Moss, 1955). However much of the original forest is now replaced by farmland. The region is dotted with numerous wet depressions, dugouts, sloughs, ponds, and a few larger lakes, all of which have marshes associated with them. Figure 1 depicts the main features of the study area.

The term "marsh" is here taken in Moss's sense (1953), meaning a grass-sedge-rush community, without moss or peat accumulation, and with a floor covered with water for one or more months of the growing season. Moss (1953, 1955) provides excellent accounts of the plant associations of such habitats.

Sites covered in this study were classified in two groups: sampling sites, used in studying carabid distribution over habitats and population dynamics; and collecting sites, used to obtain specimens for experiments and dissections. Collecting was kept to a minimum at sampling sites. Additional marshes were also sampled in a regional survey of wing dimorphism. Geographical locations

Figure 1. Map of the George Lake area, showing study sites (dots numbered 1 to 20). See Appendix I for key to site numbers. Sites 13 to 15 are outside the map; see section 3.2.5 (Chapter 3) for their exact locations.


15'
10'
114°05'W
N
16
17
Field station
George Lake
1
2
3
4
6
5
19
10
9
8
7
11
20
53°55'N
FARMLAND
FOREST
MARSHES
12
scale
0
1
2
3 KM
18

of the sites are mapped on Figure 1. A key to site numbers appearing on the map and details of the work carried out at each site are provided in Appendix I.

Sampling sites were chosen primarily on the basis of similarity in broad vegetational make-up, and of accessibility to marshes. Selected marshes had a distinct zone of sedge grass (*Carex*), one of cattails (*Typha*), and a body of open water in the middle. This follows Moss's (1953) description of the spatial succession of vegetation typical of eutrophic marshes in Alberta. This arbitrary selection procedure relative to carabid habitats was necessary to ensure some uniformity in the marshes sampled. The criterion of accessibility usually involved being able to wade to the cattails, which often formed a floating mat (see Chapter 2).

Differences among marshes, habitats and sampling programmes are described in Chapter 2.

1.3.2 Climatic conditions

Climate in central Alberta is markedly continental. Weather patterns in the study region usually bring the beginning of spring thaw in mid-April (Longley, 1967), and water bodies are normally completely thawed out by early May. The 1979 field season was about average in temperature and precipitation. However in 1980, spring arrived in March; by mid-April, all marshes and lakes were free of ice, and carabids were already active at that time (as compared to the second week of May in 1979); autumn frost began at normal time. Thus carabid population dynamics were advanced by almost a full month in 1980, and benefited from a longer than usual warm season.

A spring drought in 1980 persisted until the end of May, and many small marshes in the study area dried completely. Fortunately, water level at the main study sites did not drop significantly, and sampling was not affected.

2. HABITAT AND MICROHABITAT USE

2.1 Introduction

Detailed habitat studies of co-occurring congeners are rare in the voluminous carabid literature, in spite of numerous laboratory works exploring responses of carabids to abiotic factors and trying to link these to field distributions (see Thiele, 1977 for a comprehensive review of works on such relationships). Yet a careful examination of within- and across-habitat distribution patterns is basic to any attempt to explain factors regulating habitat occupancy and permitting coexistence. Differential use of space, promoted by habitat heterogeneity or patchiness, has, more frequently than any other niche dimensions, been correlated to coexistence patterns (Schoener, 1974).

Among the few thorough investigations of intra-habitat carabid distributions are works by Andersen (1969), Carter (1971) and Spence (1979a) which documented differences in microhabitats of co-occurring *Bembidion*, *Patrobus* and *Nebria*, respectively. Also Dawson (1965) working on fenland *Agonum* and *Pterostichus* found that peak abundances of species were differentially related to various plant communities of the fen. Murdoch (1966a) observed that *Agonum* and *Pterostichus* distributions were related to differences in soil moisture level within a marsh, with *Agonum* being restricted to wettest places.

With its ten species, the rich *Europhilus* fauna of marshes in the George Lake area offers an interesting situation for examining problems of species packing from a habitat perspective. Interesting comparisons can also be drawn from the studies of Dawson and Murdoch, both carried out in England; they cover two *Europhilus* species, of which one, *A. thoreyi*, is commonly represented in central Alberta and in the study area.

Besides questions of resource partitioning, the study of habitat use by marsh carabids provides another pedagogic opportunity in that it can help to gain insights as to how epigaeic insects like carabids cope with inundated habitats.

In this chapter, I explore the distribution of marsh carabids over habitats and microhabitats, with particular emphasis on dominant species of *Agonum*. The objective is to assess how species segregate along spatial niche dimensions and whether patterns of partitioning are altered when species composition changes.

2.2 Material and methods

2.2.1 Macrohabitat and microhabitat recognition

Five subzones were distinguished within the marsh ecosystem on the basis of dominant plant species and of presence or absence of inundation. Subzones regarded as macrohabitat categories were: (1) wet forest margin, (2) unflooded sedge meadow, (3) flooded sedge meadow, (4) emergent sedge tussocks, (5) floating cattails. The classification resembles that of Carter (1971), who employed it in a study of *Patrobus* species at George Lake, but differs in terms and in one category. The plant composition is summarized in Table 2, and a sketch of the marsh habitat succession is presented in Figure 2. Carter (1971) provides a more detailed description of each marsh subzone.

Microhabitats constituted distinct features within macrohabitats and were investigated in the flooded portion of the marsh (i.e. flooded sedge meadow, sedge tussocks and cattails). Three categories were considered: (1) recumbent dead growth –dense and sparse patches were distinguished both in the cattails and in the flooded sedge meadow; (2) emergent substrate –presence or absence of such substrate was recorded in the cattails; (3) type of sedge tussocks –tussocks of *Carex aquatilis* and of *C. rostrata* were sampled separately and considered as two distinct subcategories of the sedge tussock macrohabitat zone. Further details about macro- and microhabitats are provided in the Results

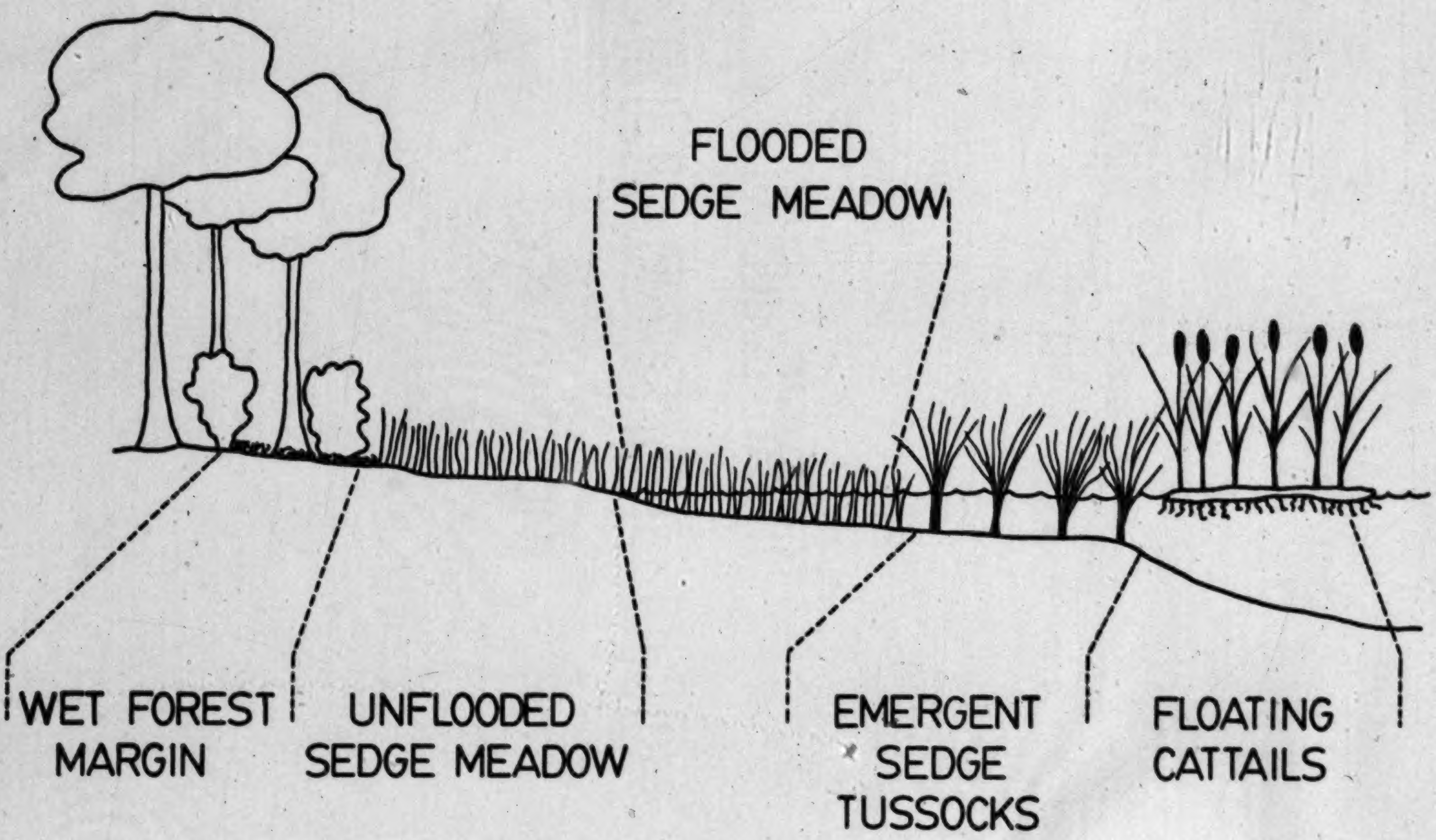
TABLE 2

Marsh macrohabitat classes
and their characteristic vegetation

MACROHABITAT DENOMINATION	DOMINANT PLANT SPECIES	CARTER'S (1971) DENOMINATION
wet forest margin	*Populus tremuloides* Michx. *Populus balsamifera* L. *Cornus stolonifera* Michx. *Salix* sp.	forest margin[1]
unflooded sedge meadow	*Carex rostrata* Stokes *Carex atherodes* Spreng.	sedge meadow[1]
flooded sedge meadow	*Carex rostrata* Stokes *Carex atherodes* Spreng.	sedge meadow[1]
emergent sedge tussocks	*Carex rostrata* Stokes *Carex aquatilis* Wahl.	shallow marsh
floating cattails	*Typha latifolia* L.	deep marsh

[1] Carter (1971) collectively classified these habitats as "transition zone", in which he also included "*Salix* habitats". The latter being completely flooded during the course of this study and not differing much from the surrounding sedge meadow was not distinguished from it.

Figure 2. Cross-section outline of macrohabitat zones of a typical marsh of the study area.


FLOODED SEDGE MEADOW
WET FOREST MARGIN
UNFLOODED SEDGE MEADOW
EMERGENT SEDGE TUSSOCKS
FLOATING CATTAILS

section.

2.2.2 Sampling method and abundance estimates

A preferred sampling technique among students of carabids is the pitfall trap, which has been used in virtually all population studies of carabids since its introduction by Barber in 1931 (see Thiele, 1977 and Adis, 1979 for reviews). However numerous biases, limitations and problems in interpretation of data await the researcher who attempts to estimate distributions and abundances from pitfall catches (Adis, 1976, 1979; Southwood, 1966: 195).

The mere fact that up to 75% of the marsh area was inundated habitat prevented the use of pitfall traps during this study. The difficulty of sampling was also compounded by the three-dimensional structure of the vegetation as a habitat, which varied in complexity (dense or sparse, tall or short, thick or thin) among macro- and microhabitats. Time-catch samples over standard areas were tried on several occasions in 1979 in the different macrohabitats, but were too inconsistent to be worthwhile. Too little time was available in the course of this study to devise a good relative technique and to calibrate it with an absolute method (as suggested by Southwood, 1966: 179). Therefore the absolute method of abundance measurement described below was adopted because it was simple. Despite a low time efficiency, the data return per unit effort was surprisingly good.

In flooded areas, quadrat counts were made with a 0.25 m^2 sampling box constructed from 3/16" clear acrylic plexiglass, with top and bottom missing. Sides of the box were 50 cm high. Metal corners bolted inside all angles near the upper and lower edges increased strength. Handles affixed on two sides facilitated carrying.

Samples were taken by wading to a randomly determined location and by inserting the box in the vegetation down into the water. With grass shears, plants and roots lapping the bottom edge of the box were cut to allow it to fit tightly to the bottom substrate. When tall, the top half of the vegetation was clipped and thrown away. The remaining vegetation in the box was cut at its base under water, immersed and stirred gently for several minutes. If the water was too shallow, more water was added with a bucket. Carabids were picked as they floated, swam or crawled along shoots to the surface, and transferred into a plastic bucket. When more than three minutes had elapsed with no other carabid showing up, waiting time was terminated and collected beetles were tallied. All adult carabids were identified to species, sexed and then released (only *Agonum* were tallied in 1979). Teneral condition was also noted when seen. For all *A. nigriceps*, wing condition was also assessed. Undetermined or uncertain specimens were placed into vials and returned to the laboratory for positive identification (less than 0.5% of all catches). Carabid larvae were also brought to the laboratory and preserved in

70% ethanol.

In unflooded areas, the plastic box was replaced by a 0.25 m², 1/8" thick aluminium box with sides 30 cm high. Lower edges of the sides were sharpened. At a randomly determined sample location, the box was pressed to the ground and the soil around the outside of the base was slotted with a shovel. The box was then pushed further down into the groove by stepping on its upper edges. These operations were done very quickly before disturbed carabids could escape. Following this, upright plants were clipped and removed and the box was filled with strained marsh water. From there on, the ritual proceeded as for samples in flooded areas.

In 1979, series of ten samples were taken in each macrohabitat during each sampling block. In 1980, five quadrat counts were made in each macrohabitat at each site on each sampling date.

Absolute estimates of abundance per unit area provided by the sampling method are probably biased towards underestimation of actual numbers. This is because some beetles may have remained trapped among the immersed vegetation and not have had enough time to escape before the waiting period for a current sample was terminated (on average, 5-10 minutes, but sometimes up to 15-20 minutes in very dense cattail vegetation). This certainly explains low catches of larvae: only about 200 were collected during the two seasons over all habitats at all sites. Larvae were more sluggish than adults; on the water they were poor swimmers and dense duck weed hampered their movements. Extraction in Berlese funnels was attempted in 1979, but the drying and extracting time per sample was beyond reasonable limit.

2.2.3 Sampling programme

The 1979 sampling programme was mainly exploratory. It aimed at adjusting the sampling method and at documenting habitat factors to which *Agonum* distributions could be related. Sites covered included Lake 1, Lake 2, Lake 4, Lake 5, Field 1, Field 2 and Field 3 (see Fig. 1 and Appendix I). They were mainly chosen for their proximity to the field station. Field 3 was abandoned in the middle of the summer because of increasing inaccessibility owing to rising water, and because of very low population levels possibly due to farm pollution.

Sampling was carried out between May 17 and September 13 in 1979 and covered only the cattails and the flooded sedge meadows at all sites. Possible microhabitat features were established and recorded at each sample location. By the middle of the summer, it became obvious that *Agonum* distributions in the sedge meadow and in the cattails could be related to presence of dead growth heaps and of emergent substrate. However no microhabitats were recognized within sedge tussocks, and all tussocks were classified as one microhabitat of the sedge meadow at that time.

An attempt was made to visit all sites within a relatively short period of time (3-5 days) at regular intervals across the season, in order to follow population fluctuations. However this proved impossible owing to unexpectedly lengthy durations of sampling.

In 1980, the programme was designed to yield both population dynamics data (Chapter 3) and more complete macrohabitat data. Therefore sampling was restricted to two study sites. These are Lake 1 and Lake 2 (combined because adjacent, and thereafter referred to as "George Lake") and Barrhead. Both sites were selected over the previous year's sites because they afforded very extensive marshes with large *Agonum* populations. Given their size, these marshes had little chance of being severely affected in case of drought. Choice of Barrhead was also motivated by the discovery of a species of *Europhilus* occurring there in significant numbers while being very scarce at George Lake. Thus these sites offered an interesting comparison between communities in light of a study on resource partitioning. Barrhead differed from George Lake by the lack, on much of its perimeter, of aspen forest surrounding the sedge meadow. Instead mesic-xeric grass vegetation bordered the latter.

Sampling in 1980 extended from May 15 to September 12. The whole range of macrohabitats was sampled at regular intervals throughout the season at both sites, within 2-3 days. Two microhabitats were also re-studied: sedge tussock samples were divided according to tussock type, and this was tallied from mid-June to September; dead growth patches were re-sampled on July 2 by taking twenty-five samples in each of the dense and sparse patches.

In the analysis of data of section 2.3, distributions over macrohabitats are based on 1980 only. Results of both years are presented for microhabitats.

2.2.4 Treatment of the data

To estimate densities, quadrat counts were averaged for each species after an increment by 1 (to avoid log 0) and conversion to natural logarithms. Transformation was necessary to damp variances and allow more meaningful parametric statistical tests. Sexes were pooled in the analysis. Densities are all presented in number per 0.25 m^2. Figures are not expressed in customary density per m^2 because multiplication of the means by 4 would entail multiplying variances and standard errors by 16, a course of action that would artificially obscure many significant differences on the graphs.

2.3 Results

2.3.1 Composition of marsh carabid fauna

A total of 2743 carabid individuals representing 25 species were tallied at George Lake and Barrhead study sites during the 1980 period. Since this study focused on *Agonum*, only carabid species equal in size to or larger than *Agonum* were recorded. Groups such as *Bembidion*, *Trechus* and *Bradycellus* were ignored in the samples. Because of their much smaller size than *Agonum*, they are likely to occupy quite different niches and not directly interact with bigger carabids, except perhaps as prey.

Table 3 presents numbers of specimens tallied and relative abundances of all species at both marshes. Among these, 8 species are *Europhilus* members, 7 of which (excluding *A. retractum*) are marsh dwellers. *A. nigriceps*, *A. ferruginosum* and *A. thoreyi* markedly dominate the carabid community, accounting for about 86% of the total catch at either site. *A. lutulentum* also constitutes a significant proportion of the catch at Barrhead. The community is poorer by 9 species at Barrhead.

Most of this study will therefore focus on aspects of the ecology of the four dominant *Agonum* (*Europhilus*) mentioned above.

TABLE 3

Species of carabids sampled at the two main study sites in 1980, and their relative abundances

SPECIES	GEORGE LAKE		BARRHEAD	
	N	%	N	%
*Agonum nigriceps**	390	22.6	289	28.5
*Agonum ferruginosum**	726	42.0	250	24.6
*Agonum thoreyi**	373	21.6	330	32.5
*Agonum lutulentum**	5	0.3	109	10.7
Agonum propinquum	40	2.3	6	0.6
Agonum mannerheimi	23	1.3	0	---
Agonum affine	33	1.9	3	0.3
*Agonum superioris**	38	2.2	7	0.7
*Agonum sordens**	6	0.3	1	0.1
*Agonum gratiosum**	7	0.4	4	0.4
Agonum anchomenoides	4	0.2	0	---
Agonum decentis	5	0.3	0	---
*Agonum retractum**	1	0.1	0	---
Patrobus stygicus	35	2.0	6	0.6
Patrobus lecontei	4	0.2	1	0.1
Patrobus septentrionis	1	0.1	0	---
Pelophila rudis	3	0.2	0	---
Blethisa multipunctata	2	0.1	1	0.1
Loricera pilicornis	8	0.5	0	---
Elaphrus clairvillei	2	0.1	1	0.1
Pterostichus patruelis	19	1.1	3	0.3
Pterostichus pensylvanicus	1	0.1	0	---
Pterostichus corvinus	1	0.1	2	0.2
Carabus maeander	0	---	2	0.2
Amara sp.	1	0.1	0	---
TOTALS	1728		1015	

* denotes a member of *Europhilus* (*sensu* this study)

2.3.2 Species distribution in relation to inundated areas

Inasmuch as marshes provide a habitat for epigaeic carabids, their most conspicuous structural characteristic is the inundated zone. During years of normal or high precipitations, the flooded zone usually covers a large portion of the marsh (up to 80% at the main study sites), and it may be expected to affect carabid distribution.

The percentage of total captures accountable to each species was calculated for both flooded and unflooded portions of the marsh. Species contributing very low percentages (<0.5%) were pooled. Figures 3 and 4 depict these frequency distributions at George Lake and Barrhead respectively. Species composition and relative abundances differed markedly between the two zones. The majority of species were confined to the unflooded zone at both marshes. In contrast, the dominant *Agonum* occurred in either zone, but were more abundant in the flooded area.

2.3.3 Macrohabitats

The five macrohabitats were from upper to lower portion of the marsh: (1) forest margin with wet to waterlogged humus and leaf litter; (2) unflooded and (3) flooded sedge meadows, the extent of which varied according to fluctuations in the water level; (4) emergent sedge tussocks, scattered in pools and in open water spreads between the cattails and the sedge meadow; (5) cattails, forming a floating mat extending at the edges of open water.

Figure 3. Relative abundance of carabid species in flooded and unflooded marsh zones at the George Lake study site. Letters below bars stand for species names as follows:

N = *Agonum nigriceps*

F = *A. ferruginosum*

T = *A. thoreyi*

P = *A. propinquum*

Su = *A. superioris*

A = *A. affine*

M = *A. mannerheimi*

So = *A. sordens*

G = *A. gratiosum*

Pas = *Patrobus stygicus*

Pal = *Pa. lecontei*

Ptp = *Pterostichus patruelis*

Lp = *Loricera pilicornis*

Pooled species are

(1) for the unflooded zone:

A. decentis, *Pa. septentrionis*, *Pelophila rudis*, *Blethisa multipunctata*, *Pt. pensylvanicus* and *Amara* sp.

(2) for the flooded zone:

A. propinquum, *A. affine*, *A. sordens*, *A. gratiosum*, *A. anchomenoides*, *A. retractum*, *A. decentis*, *Pa. stygicus*, *B. multipunctata*, *Elaphrus clairvillei* and *Pt. corvinus*.

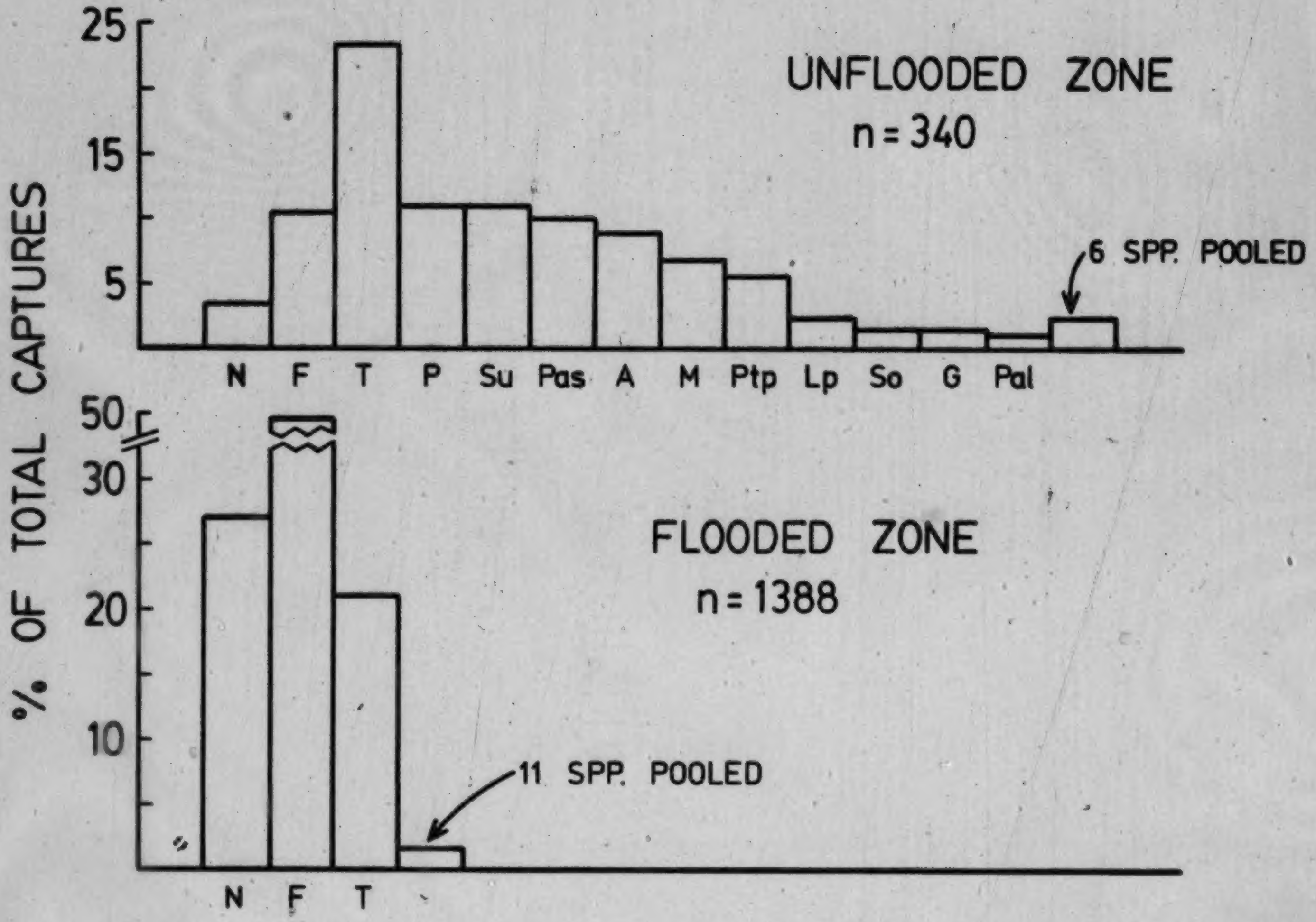

% OF TOTAL CAPTURES
25
15
5
UNFLOODED ZONE
n = 340
6 SPP. POOLED
N
F
T
P
Su
Pas
A
M
Ptp
Lp
So
G
Pal
50
30
20
10
FLOODED ZONE
n = 1388
11 SPP. POOLED
N
F
T

Figure 4. Relative abundance of carabid species in flooded and unflooded marsh zones at the Barrhead study site. Letters below bars stand for species names. See Fig. 3 for key to names, except for the following:

Cam = *Carabus maeander*

L = *A. lutulentum*

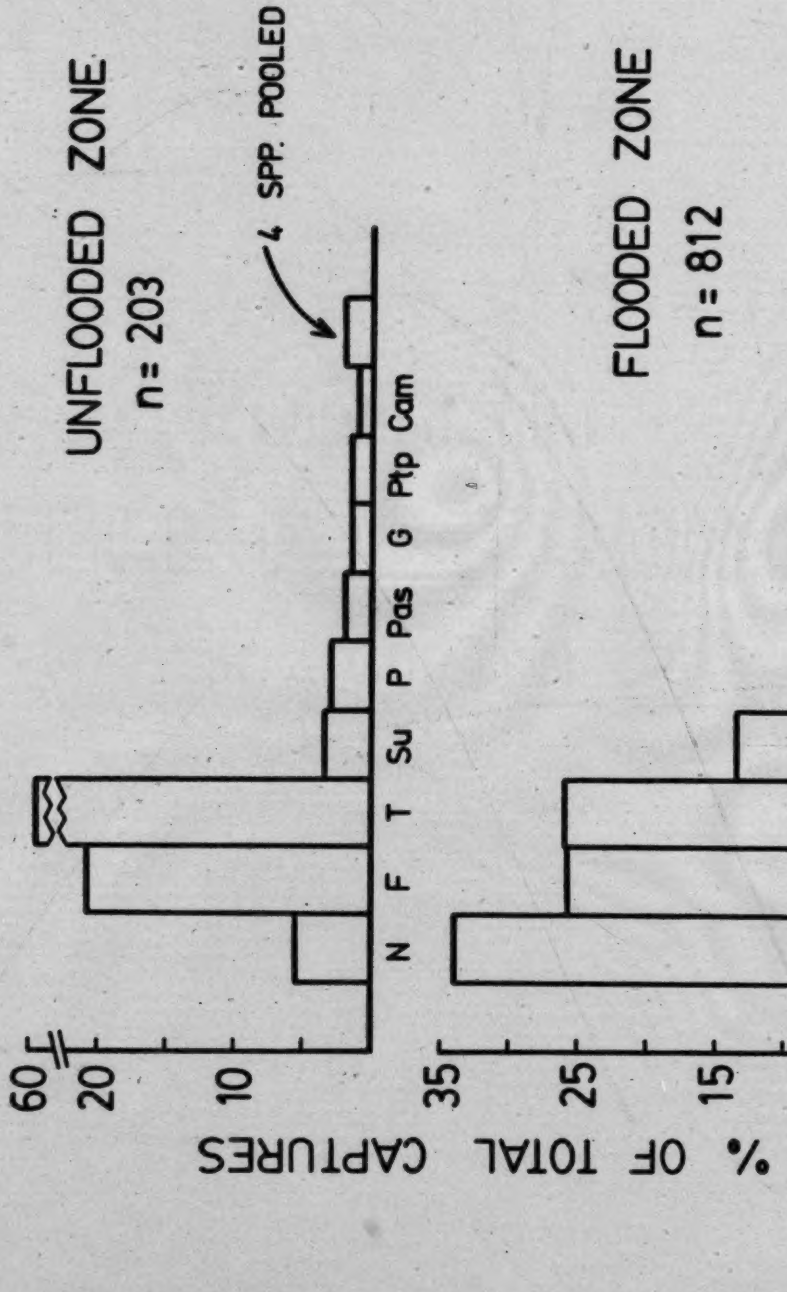
Pooled species are

(1) for the unflooded zone:

A. lutulentum, *A. affine*, *Pa. lecontei* and *E. clairvillei*.

(2) for the flooded zone:

A. affine, *A sordens*, *A. gratiosum*, *Pa. stygicus*, *B. multipunctata* and *Pt. corvinus*.


UNFLOODED ZONE
n= 203
4 SPP. POOLED
N
F
T
Su
P
Pas
G
Ptp
Cam
60
20
10
% OF TOTAL CAPTURES
35
25
15
5
FLOODED ZONE
n= 812
6 SPP. POOLED
N
F
T
L

A sketch of the marsh habitat succession is presented in Figure 2.

Average densities of the four dominant *Agonum* in each macrohabitat are presented graphically in Figure 5 and Figure 6 . At George Lake (Fig. 5), strong density peaks appeared in single macrohabitat types for two species. *A. nigriceps* was the most abundant in sedge tussocks, while *A. ferruginosum* peaked in cattails. *A. thoreyi* was spread throughout most of the marsh, though it tended to be slightly more dense in cattails. The abundance of *A. lutulentum* was too low to show a definite pattern, though this species did not occur in unflooded macrohabitats. *A. thoreyi* was the most abundant species in unflooded macrohabitats. *A. nigriceps* was absent from the forest margin.

Results were analysed with one-way analyses of variance and statistics are tabulated in Appendix II. F-values indicate highly significant differences across macrohabitats in all species, though differences are less pronounced for *A. thoreyi*. Despite heterogeneity of variance partly invalidating the analyses (Bartlett's test: probability of homogeneity of variances <0.01 in all cases), the great magnitude of discrepancies among means indicates real differences.

At Barrhead (Fig. 6), marked association peaks were also observed in three species with respect to particular macrohabitats. *A. nigriceps* and *A. lutulentum* were both most

Figure 5. Densities of species of *Agonum* in various marsh macrohabitats at the George Lake study site. (Means ± 1 SE).

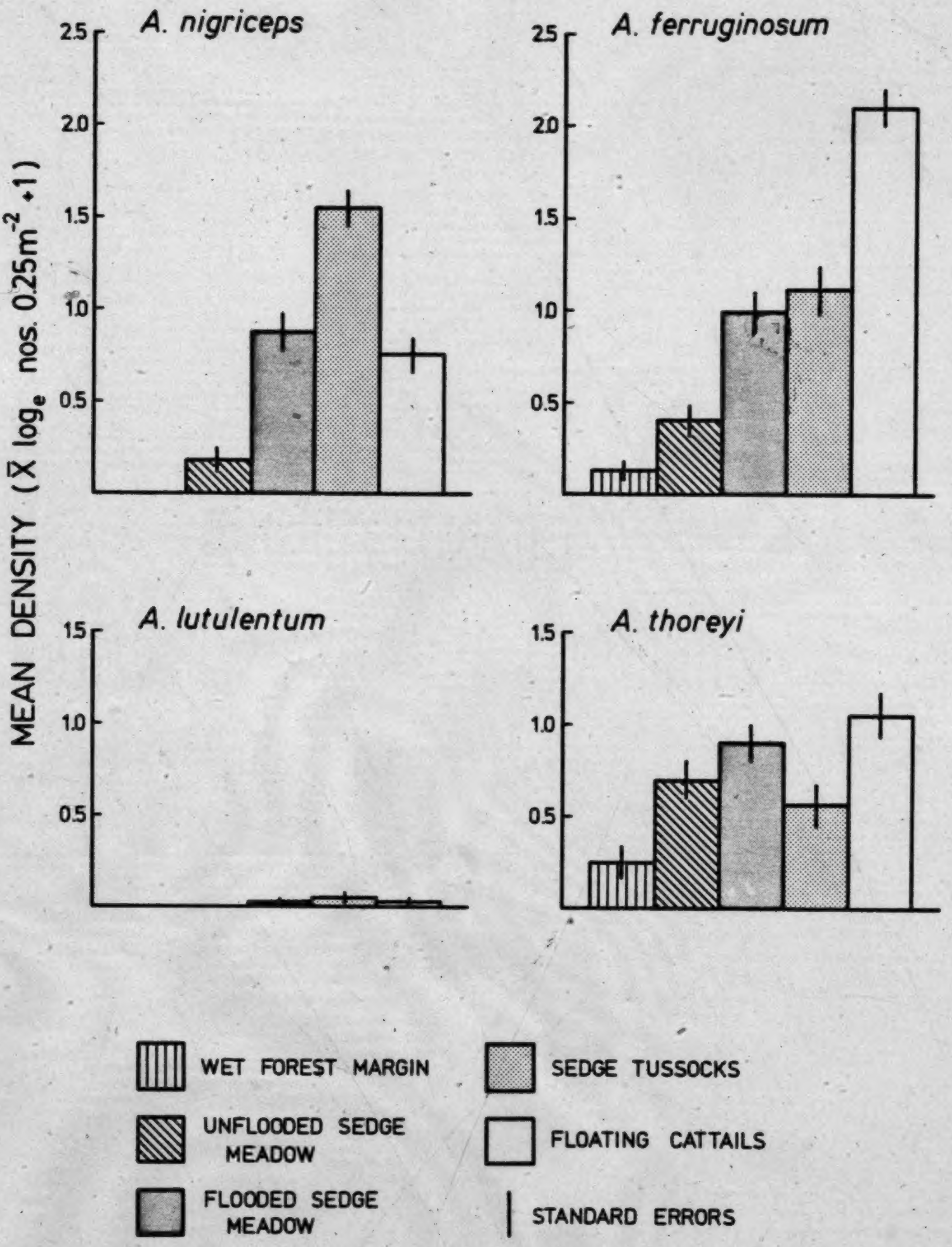
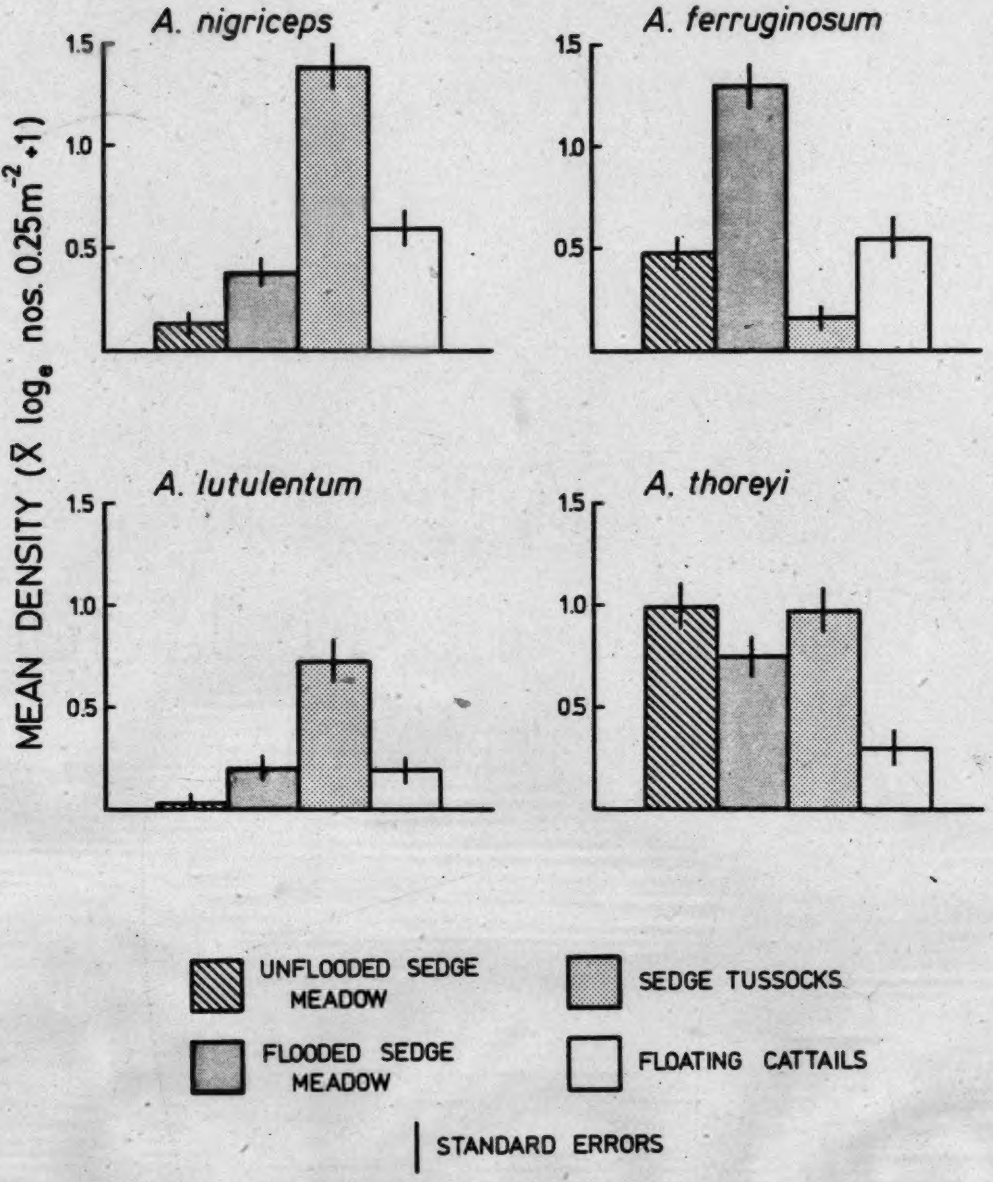

A. nigriceps
A. ferruginosum
A. lutulentum
A. thoreyi
MEAN DENSITY ($\bar{X}$ $\log_e$ nos. 0.25m^{-2} +1)
2.5
2.0
1.5
1.0
0.5
WET FOREST MARGIN
UNFLOODED SEDGE MEADOW
FLOODED SEDGE MEADOW
SEDGE TUSSOCKS
FLOATING CATTAILS
STANDARD ERRORS

Figure 6. Densities of species of *Agonum* in various marsh macrohabitats at the Barrhead study site. (Means ± 1 SE).


A. nigriceps
A. ferruginosum
A. lutulentum
A. thoreyi
MEAN DENSITY ($\bar{X}$ log$_e$ nos. 0.25m^{-2} +1)
1.5
1.0
0.5
UNFLOODED SEDGE MEADOW
FLOODED SEDGE MEADOW
SEDGE TUSSOCKS
FLOATING CATTAILS
STANDARD ERRORS

abundant in sedge tussocks, while *A. ferruginosum* was markedly associated with flooded sedge meadow. *A. thoreyi* was more or less equally distributed over three habitat zones, and was least abundant in cattails. Analyses of variance (Appendix II) revealed markedly significant differences, but again variances were heterogeneous.

Across-habitat distributions and abundance peaks were approximately the same at both marshes for *A. nigriceps*, but notable differences were observed in those of *A. ferruginosum* and *A. thoreyi*. Both species showed markedly lower densities in cattails at Barrhead as compared to George Lake; this is particularly dramatic in *A. ferruginosum* (note the logarithmically compressed scale of the figures). At Barrhead, the density of *A. thoreyi* was significantly higher in unflooded meadow and in tussocks than at George Lake. *A. ferruginosum*'s peak occurred in the flooded meadow at Barrhead as compared to the cattails at George Lake. The latter species also showed a dramatic drop in abundance in sedge tussocks coincident with higher densities of *A. thoreyi* and, more notably, of *A. lutulentum*.

The data of Figures 5 and 6 also emphasize high densities reached by the species. If log values are converted to actual numbers, average densities reach highs ranging from 7 beetles per square meter (*A. lutulentum* in Barrhead tussocks) to 33 (*A. ferruginosum* in George Lake cattails). Heterogeneity of variance persists in spite of logarithmic transformation of the data, indicating marked clumping in spatial distribution.

2.3.4 Microhabitats

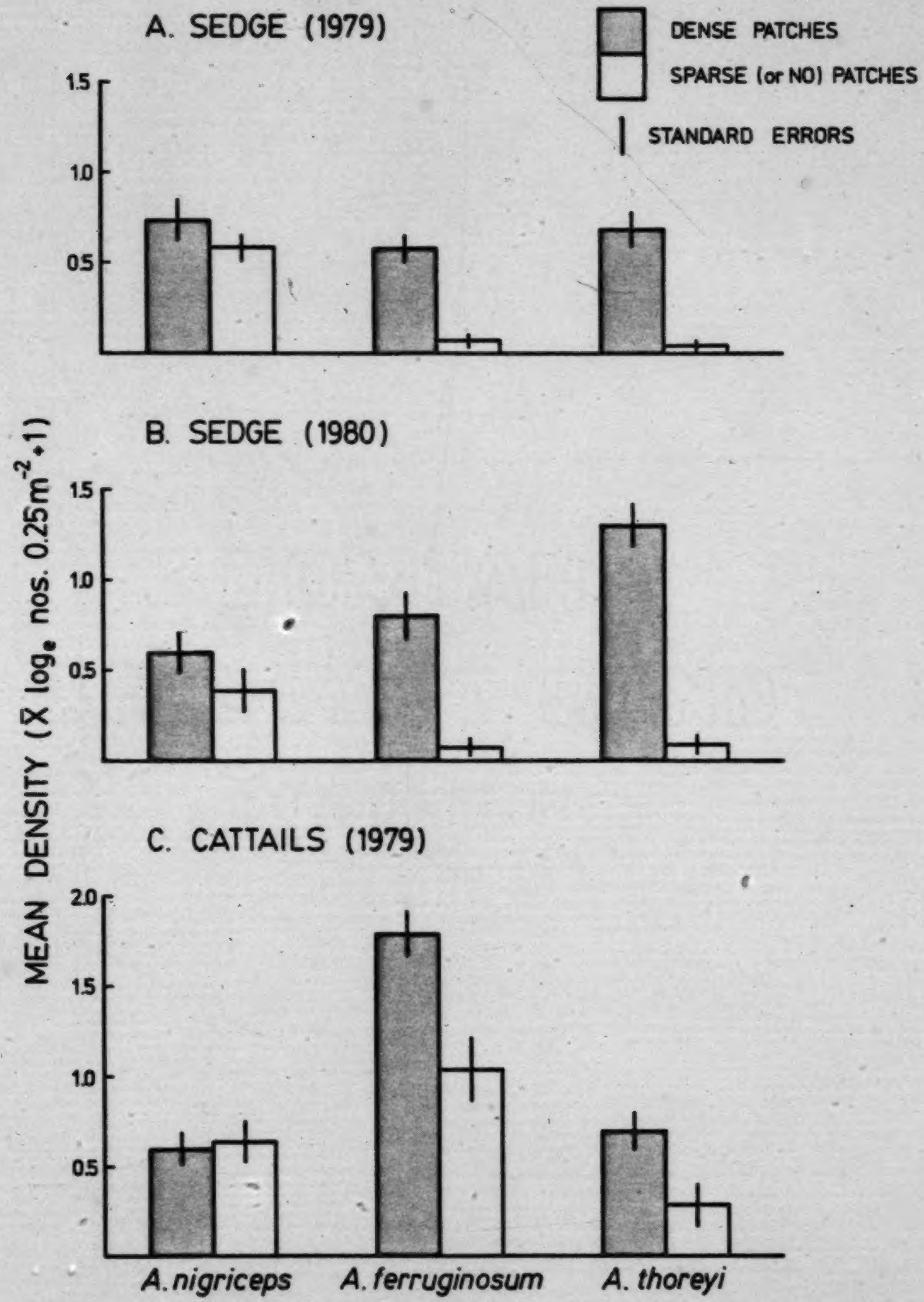
Distributions with respect to microhabitat features, presented as mean densities, were tested with analysis of variance and a summary of the statistics pertaining to all microhabitats and species is provided in Appendix III. Variances were homogeneous in most comparisons, and where not, high F-ratios indicate significant differences.

2.3.4.1 Dead growth patches

Patches of recumbent dead growth consisted of accumulation of old shoots entangled above the water at the base of growing shoots. Patches varied in size (from about 0.2 m² to a few m²) and were classified into two more or less qualitative categories. Thick or dense patches were those through which the water surface could not be seen from above, while in sparse (or absence of) patches, the water could be seen from above. These microhabitat features were studied both in cattails and in flooded sedge meadow. In cattails, some thick patches formed extremely dense heaps up to 0.5 m high.

Figure 7 shows densities of the three dominant species of *Agonum* in relation to dead growth patches, recorded at George Lake during two seasons. The data indicate that *A. nigriceps* was equally distributed over sparse or dense patches either in sedge habitats (Figs. 7a, 7b) or in

Figure 7. Distribution of species of *Agonum* in relation to patches of dead growth in sedge meadow and in cattails. (Means ± 1 SE).


A. SEDGE (1979)
DENSE PATCHES
SPARSE (or NO) PATCHES
STANDARD ERRORS
1.5
1.0
0.5
B. SEDGE (1980)
1.5
1.0
0.5
C. CATTAILS (1979)
2.0
1.5
1.0
0.5
MEAN DENSITY ($\bar{X}$ $\log_e$ nos. $0.25m^{-2}$+1)
A. nigriceps
A. ferruginosum
A. thoreyi

cattails (Fig. 7c). The slight differences are not statistically significant (see Appendix III). Conversely, distributions of *A. ferruginosum* and *A. thoreyi* appeared sensitive to patch type, as they were markedly concentrated in dense patches in either macrohabitat. Differences are highly significant when tested with one-way analysis of variance (Appendix III).

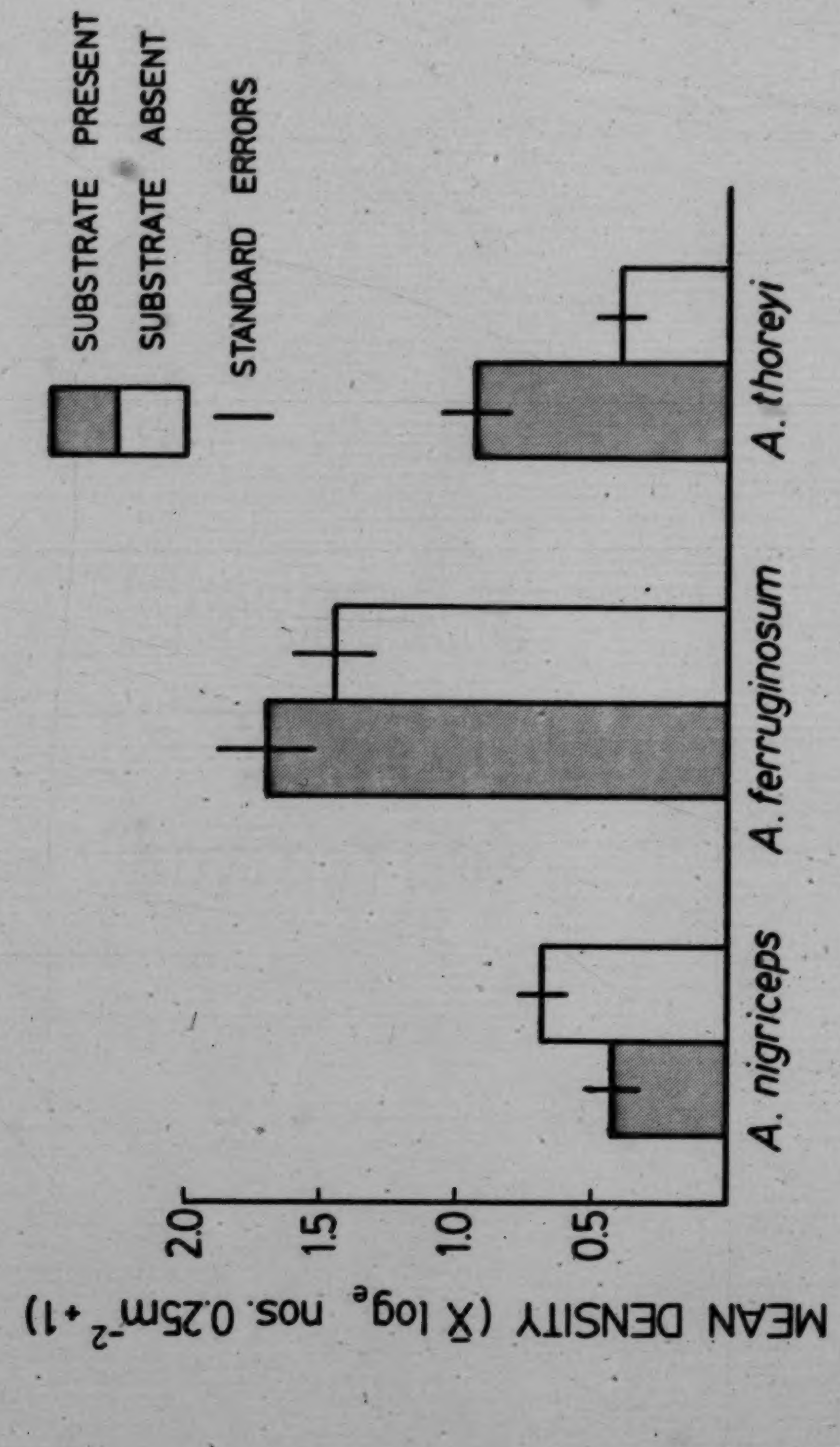
2.3.4.2 Emergent substrate

This microhabitat feature was studied only in cattails. Substrate was present where the floating mat of organic debris and roots rose above the water (often owing to logs trapped underneath), and absent where the shoot bases plunged directly into the water. In flooded sedge meadow, emergent substrate was too rarely encountered to allow sufficient sample size. Figure 8 illustrates the distributions of the main *Agonum* species with respect to substrate in the George Lake cattails. Densities of *A. nigriceps* and *A. ferruginosum* did not significantly differ in presence or absence of substrate, while *A. thoreyi* was markedly associated with areas of emergent substrate.

2.3.4.3 Sedge tussocks

Sedge tussocks differed structurally depending on the constituent species of *Carex*. Tussocks of *C. aquatilis* had very thin shoots growing at high density ($\geq$100 shoots/0.25 m^2), were encumbered with dense recumbent dead growth and stood on emergent humps formed by their root system and

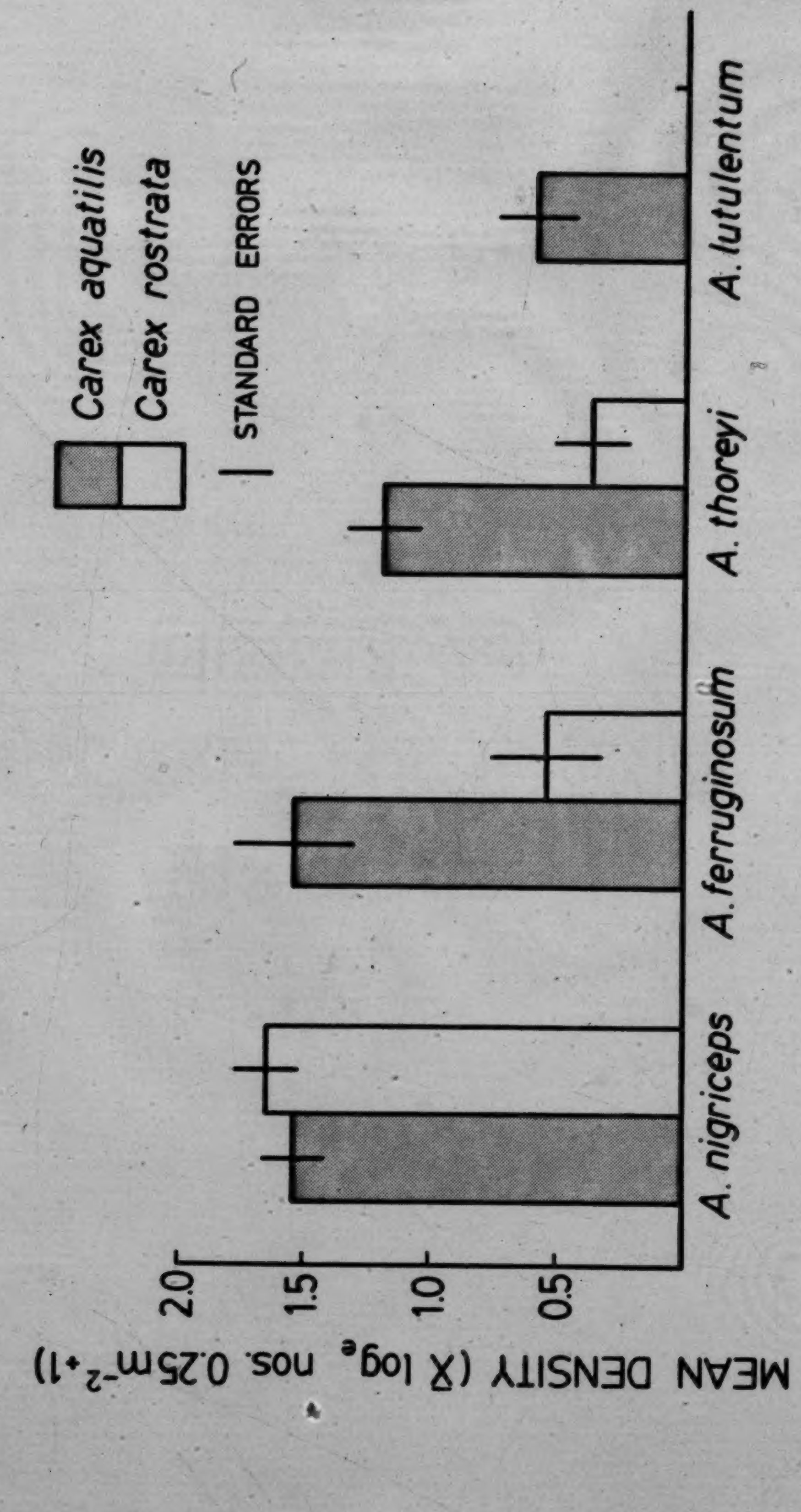
Figure 8. Distribution of species of *Agonum* in relation to emergent substrate in cattails. (Means ± 1 SE).


MEAN DENSITY (X̄ log$_e$ nos. 0.25m^{-2}+1)
2.0
1.5
1.0
0.5
A. nigriceps
A. ferruginosum
A. thoreyi
SUBSTRATE PRESENT
SUBSTRATE ABSENT
STANDARD ERRORS

accumulated organic debris. Tussocks of *C. rostrata* had thick shoots, grew quite loosely (<50 shoots/0.25 m^2), had no or sparse entangled dead growth, and no basal hump rising above the water.

Data from George Lake and Barrhead were pooled in the analysis because they did not differ significantly. Results are displayed in Figure 9. *A. ferruginosum*, *A. thoreyi* and *A. lutulentum* were all markedly associated with tussocks of *C. aquatilis*. No individual of *A. lutulentum* was even found in *C. rostrata* tussocks. In contrast, *A. nigriceps* was equally distributed over both types of tussocks.

Figure 9. Distribution of species of *Agonum* with respect to type of sedge tussocks. (Means ± 1 SE).


MEAN DENSITY (X̄ log_e nos. 0.25m^-2+1)
2.0
1.5
1.0
0.5
A. nigriceps
A. ferruginosum
A. thoreyi
A. lutulentum
Carex aquatilis
Carex rostrata
STANDARD ERRORS

2.4 Discussion

2.4.1 Inundation and species distribution

Restriction of the majority of carabid species to the unflooded portion of the marsh indicates that inundation is a factor markedly influencing the distribution of marsh carabids over their habitat. This is consistent with the fact that most carabids (at least in temperate regions) are epigaeic (Thiele, 1977).

If this result seems trivial, what is less so is the finding that some *Europhilus* species not only do not seem affected by the water-covered soil, but indeed are quite restricted to the flooded zone where they live among the emergent vegetation.

The latter observation did not result from the fact that the beetles sampled in the inundated marsh had been caught by surprise by sudden flooding, because the data were cumulative for the season; in addition the water level remained fairly stable from 1978 to 1980 at the main study sites.

Inundation causes riparian carabids to flee by swimming aground or seeking temporary refuge on floating debris and emergent plants (Andersen, 1968). With respect to marsh *Agonum*, Murdoch (1966a) observed that the European *Europhilus* species *A. fuliginosum* occupied the water edge but fled in face of rising water.

Although it is already known that some *Europhilus* species commonly occur among marsh vegetation (e.g. Lindroth, 1966: 584), this study seems to be the first to report quantitatively that the bulk of their populations can be restricted to such a habitat, and that the flooded portion of the marsh is hardly used at all by the rest of the carabid community. Confinement of most species to unflooded edges of the marsh is undoubtedly linked to difficulties that foraging on emergent vegetation may entail. However, dominant *Europhilus* species are obviously able to prosper in that portion of the habitat as evidenced by their abundance.

Carabids that efficiently exploit the flooded zone possibly benefit from an advantage in terms of population persistence during both flood and drought periods. During times of high water, their habitat expands; during drought times, it shrinks, but despite the possibility of overcrowding, high level of ambient moisture may insure the continuation of population processes. In contrast, species limited to the unflooded zone face habitat shrinking during both flood and drought periods. Periodic occurrence of harsh conditions may thus favour populations of the flooded marsh species over the long run.

2.4.2 Species distribution and microclimatic factors

Species richness (i.e. the number of species) differed strikingly between George Lake and Barrhead, the latter having a poorer fauna inhabiting its unflooded margins. This undoubtedly reflects lack of surrounding forest at Barrhead (see section 2.2.1). Presence of a forest margin can affect significantly the local microclimate at the marsh edge by casting shade, dampening daily temperature fluctuations and helping to maintain a high moisture level in the unflooded zone. These three factors are deemed to play a prominent role in affecting the distribution of many carabids (Thiele, 1964; 1977; Paarmann, 1966; Bauer, 1974) with moisture being the most critical one (Thiele, 1968), and quite likely they are important in determining which species will occupy the marsh edge.

In contrast, the relative abundances of species inhabiting the flooded zone differed little between the two marshes. Microclimate within that part of the marsh, especially the ambient moisture level, is unlikely to be markedly affected by presence or absence of forest. Unless it dries up, a relatively rare event, the flooded marsh is a habitat constantly moisture saturated (Murdoch, 1966a), especially at the base of the vegetation where the carabids occur. Thus factors other than suitable moisture levels are likely to regulate carabid distribution within the flooded zone.

The abundance of *A. lutulentum* at Barrhead, contrasting with its virtual absence at George Lake, may be related to the fact that this species is generally found in marshes of open areas (G.E. Ball, pers. comm.), which may not necessarily imply a response to microclimate but may be connected with interhabitat dispersal capabilities of the species, for example.

The drop in species richness at Barrhead emphasizes the restriction imposed by inundation on the distribution of most carabid species within the marsh. Otherwise, if inundation was unimportant, hygrophilic carabids facing reduced moisture conditions should be able to move and occupy the flooded zone, which affords humidity and shelter through its luxuriant vegetation.

2.4.3 Vegetation structure, habitat segregation and coexistence

The data demonstrate relatively ample spatial separation among the dominant *Europhilus* species at both macro- and microhabitat levels. Habitat associations of the species appear to be more or less arrayed along a generalist-specialist continuum with some complementarity relative to the two main habitat levels. *A. thoreyi* is the most general with respect to macrohabitats but has the most restricted distribution relative to microhabitat features. *A. ferruginosum* and *A. nigriceps* can be regarded as macrohabitat specialists with peaks occurring in different habitat classes. *A. ferruginosum* is however fairly restricted in microhabitats, while *A. nigriceps* is a microhabitat generalist. Thus *A. ferruginosum* occupies an intermediate position between *A. nigriceps* and *A. thoreyi*. *A. lutulentum* is a macrohabitat specialist whose distribution matches closely that of *A. nigriceps*, but spatial data on its microdistribution suggest that it could be a microhabitat specialist.

Habitat associations such as these do not allow any conclusion on preference or selection of habitat by any of the species studied. Experiments are needed to establish that individuals of a species exercise active habitat selection (Klopfer, 1969: 40ff) and that observed field distributions are not the result of other processes such as interspecific interactions or differential predation. However the present data suggest interesting hypotheses about some of the factors that may regulate the within-habitat distribution of marsh *Agonum*.

2.4.3.1 Vegetation structure

Distributions of the dominant *Agonum* species in the flooded marsh zone appeared sensitive to the vegetation features that were employed to define macro- and microhabitat classes. Because these carabids forage among the vegetation, it is likely that they are affected by the structural characteristics of the emergent plants. The various macro- and microhabitat categories afford different degrees of structural complexity which may alleviate or impair foraging efficiency in ways different for each species. For example, areas of flooded sedge meadow without dead growth or tussocks of *C. rostrata* present a relatively simple, open structure of upright stalks with a few bent leaf blades, in which foraging may be seriously hampered for members of a species not adapted for climbing and walking on narrow plants. In contrast, heaps of dead cattails form a dense web of plants in which climbing may not be a necessity for ensuring efficient foraging.

Evidence supporting the hypothesis on the importance of vegetation structure is provided by a shift in the peak habitat of *A. ferruginosum* and *A. thoreyi* between George Lake and Barrhead. Both species were common in the cattails at George Lake, but were virtually absent from that habitat at Barrhead. These two species are mainly associated with dense patches of dead growth, and for *A. thoreyi*, with emergent substrate. These microhabitat characteristics were generally lacking in the Barrhead cattails. In contrast, *A. nigriceps*, whose distribution is independent of these microhabitat features, occurred at about equal densities in the cattails at either marsh.

Differential responses to simple structural attributes of the vegetation which explain microhabitat differences have been shown in lycosid spiders hunting on plants (Greenquist and Rovner, 1976) and in water-striders (Spence, 1979b). It is possible that microhabitat sites of flooded marsh *Agonum* are, at least partially, determined by similar responses. Experiments on habitat selection might well begin by exploring these possibilities.

2.4.3.2 Competition

One of the most interesting findings of this study pertains to the presence of *A. lutulentum* at Barrhead, which shows its peak abundance in sedge tussocks. Coincidentally *A. ferruginosum* occurred at low density in these tussocks, in marked contrast with its abundance at George Lake in the same macrohabitat. This pattern suggests that *A. ferruginosum* may be competitively displaced by *A. lutulentum*. Of course, this could be explained on other grounds. For instance it might be argued that undetected differences in habitat conditions (which were looked for but not found) favourable to *A. lutulentum* but not to *A. ferruginosum* caused the observed pattern. Although this possibility cannot be denied, it must also account for the fact that both *A. nigriceps* and *A. thoreyi* have remained unaffected. Thus in light of present evidence, it is more parsimonious to hypothesize competitive effects to explain the observations.

A similar pattern of negatively correlated distributions is reported by Spence (1979a) for *Nebria* larvae, for which competition has also been suggested as a likely explanation. This type of evidence is only circumstantial, but it fulfills the first empirical criterion necessary for suggesting competition in field populations (Reynoldson and Bellamy, 1971). Other empirical support necessitates use of a common resource such as food, a definite possibility in the present comparison given the opportunistic food habits of these carabids. However a competition explanation must remain speculative until it is tested experimentally, preferably through field manipulations (Connell, 1975). The possibility of competitive interactions between *A. ferruginosum* and *A. lutulentum* will be re-examined in Chapter 5 in conjunction with body size differences.

2.4.3.3 Density compensation

The high densities reached by populations of marsh *Agonum* are certainly their most striking attribute (Murdoch, 1966a). This situation is not unique to carabids however; spiders were also very abundant in marshes of the study area.

At least two factors may explain high densities, particularly in relation to the flooded portion of marshes. First, occupation of the vegetation by carabids entails exploitation of a three-dimensional habitat, in contrast to the two-dimensional ground generally inhabited by carabids. Therefore the marsh allows for an expansion of niche space by addition of an extra habitat dimension. Second, the flooded zone may afford more stability in critical factors such as humidity. These characteristics combined with a high organic productivity probably confer to eutrophic marshes unusually high carrying capacities for invertebrates, which may elicit proportionate population responses by carabids and other hunting arthropods like spiders.

A. ferruginosum and especially *A. thoreyi* showed markedly higher densities in unflooded zone at Barrhead compared to George Lake. This pattern is correlated with the lower species richness at Barrhead, and is suggestive of the phenomenon of density compensation (MacArthur *et al.*, 1972). This may come about when presumed diffuse competition (i.e. the moderate competitive effects brought upon one species by a cluster of other species —MacArthur, 1972b: 29) is relaxed. Boer (1971) has presented a populational model, based largely on data on carabids, in which analogous effects coupled with habitat heterogeneity could operate to determine population densities. The present data suggest that population responses to lower species richness are possible in marsh carabids.

In conclusion, the dominant marsh guild members displayed significant spatial differentiation that may help account for their coexistence.

3. PHENOLOGY, DAILY ACTIVITY AND ALARY MORPHISM

3.1 Introduction

Time of activity can be rightly regarded as a niche dimension along which potential competitors can be spread (Pianka, 1978: 251). For terrestrial poikilotherms, food partitioning through differential timing of daily activity is quite frequently observed possibly because heterogeneity of the environment on a small time scale is high for these animals (Schoener, 1974).

Seasonal differentiation is another way for species occupying the same habitat to avoid each other. This is also fairly commonplace in invertebrates, probably because short generation times permit them to partition the year more finely than animals whose maturing periods are relatively longer (Schoener, 1974). Even slight differences in timing of life cycle could lead to important consequences affecting the relative success of all congeners in a guild.

Seasonal activity and abundance, breeding periods and daily activity rhythms constitute very fashionable areas of study among carabidologists, judging by the bulk of papers related to these topics (reviewed in Thiele, 1977: 225ff). Pioneered by Larsson (1939), such investigations have been mainly concerned with general characteristics of life cycles of carabids, and have attempted to classify taxa with respect to broad categories of annual rhythms such as spring vs autumn breeders, larval vs imaginal hibernators, etc. (e.g. Larsson, 1939; Gilbert, 1957, 1958; Schjøtz-Christensen, 1965; Murdoch, 1967; Barlow, 1970; Bousquet and Pilon, 1977; Thiele, 1977: 246ff). Aspects of the natural history of taxonomically related (sometimes, but not always, co-occurring) carabid species have been explored mainly through comparisons of life cycles and activity patterns (e.g. Gilbert, 1956; Johnson *et al.*, 1966; Murdoch, 1966a; Barlow, 1970; Carter, 1971; Goulet, 1974; Wäsner, 1979). However such comparisons are rarely coupled with extensive or detailed habitat data (among the few: Dawson, 1965; Andersen, 1969; Spence, 1979a). Moreover, workers have generally been content with documenting differences in phenology in a broad manner (e.g. spring vs autumn breeders). Breeder types, for instance, are frequently perceived in terms of maximization of survival in relation to seasonal changes in habitat and in environmental factors, or to geographical locations and climatic patterns (Lehmann, 1965; Murdoch, 1967; Thiele, 1977: 248). Likewise, differences in daily activity patterns have been interpreted mainly in relation to habitat and to light-dark preferences (Thiele, 1964, 1977: 239, 1979; Thiele and Weber, 1968).

Though the generality of such ecological considerations is necessary for understanding broad ecological and geographical patterns, they are probably much less important for the study of intra-community coexistence. If time differences are to play any role in coexistence, especially among close relatives, it is likely to be on a small scale rather than in general aspects. For example, small discrepancies in breeding periods coupled with differences in fecundity could significantly affect the specific patterns of resource exploitation by larvae, and ultimately, species success. It is only recently that implications for coexistence of small-scale differences in life history and reproduction (Wasner, 1979) and in daily foraging pattern (Spence, 1979a) began to be considered.

In this chapter, I examine temporal segregation among the dominant species of marsh *Agonum*, both on the daily and annual scale, through comparisons of population dynamics, reproduction, emergence and daily locomotory activity. The objective is to assess whether differences in timing can contribute to the mechanisms of coexistence of this guild. The problem of wing dimorphism of *A. nigriceps* and *A. ferruginosum* is also explored from a regional perspective. It is addressed here because it implies dynamic aspects of habitat colonization and population survival in time.

3.2 Material and methods

3.2.1 Seasonal abundance

Changes in overwintered and teneral adult populations of *A. nigriceps*, *A. ferruginosum* and *A. thoreyi* were monitored at both George Lake and Barrhead. Populations of *A. lutulentum* were followed at Barrhead only. From mid-May to mid-September 1980, sampling was carried out at approximate 15-day intervals using the sampling procedure described in Chapter 2. All macrohabitats at both sites were equally sampled (five quadrat counts/habitat) within 2-3 days. Log transformed counts were used to calculate mean absolute densities (see section 2.2.4) and to generate population curves for overwintered and teneral adults.

3.2.2 Recognition of teneral adults

Specimens with pale-soft cuticle, or with tanned body but still flexible elytra, were both recorded as tenerals. All other adults were recorded as overwintered.

3.2.3 Condition of ovaries

Twenty females each of *A. nigriceps*, *A. ferruginosum* and *A. thoreyi* were collected and preserved in 70% ethanol at approximate 10-day intervals from April 19 to August 28, 1980. Collecting sites are indicated in Appendix I. Females of *A. lutulentum* were not collected because the only known significant population of this species was at the Barrhead site, and it was feared that removal of females could affect data about population dynamics obtained at the same time.

Collected specimens were subsequently dissected and condition of the ovaries was assessed. Following criteria used by Gilbert (1956) and by Vlijm and van Dijk (1967), four classes were recognized: (1) ovaries with developing ovocytes but without mature (chorionated) eggs, (2) ovaries with chorionated eggs, (3) ovaries without eggs and with corpora lutea (so-called "spent" by Gilbert, 1956), and (4) ovaries undeveloped (sexually immature). No distinction was made between one-year and two-year old females.

The number of mature eggs per female was counted and used to estimate egg laying periods and assess the breeding times of species. Justification of this approach in lieu of direct observation of oviposition is fully discussed in Murdoch (1966a).

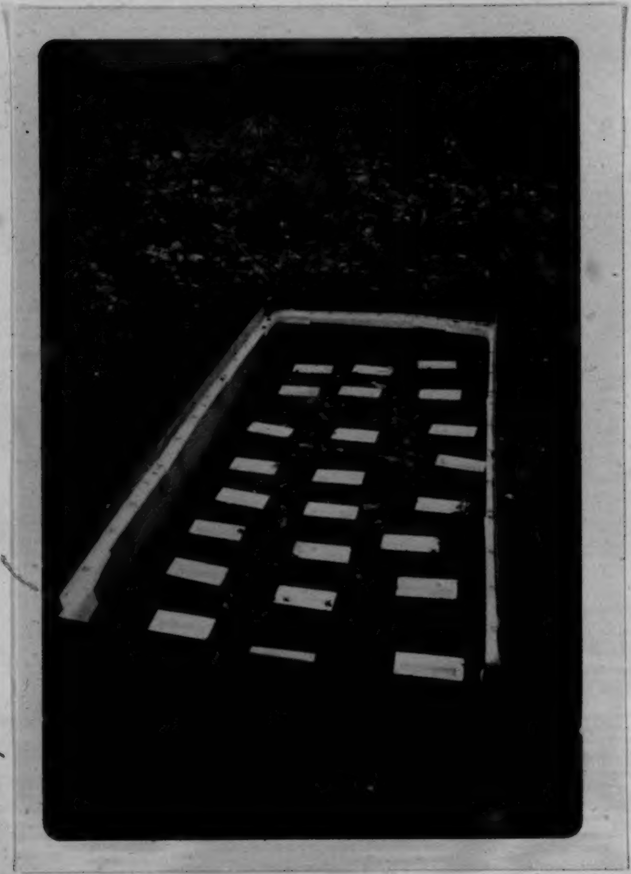
3.2.4 Enclosure experiment for daily activity

Daily activity was studied in a somewhat simplified environment. A rectangular enclosure, 2.0 x 1.0 m, was built in a small clearing of the wet forest margin at the edge of the sedge meadow (Lake 2 site). The sides of the enclosure were made of 1/4" plywood and were 30 cm high. They were inserted 3-5 cm into the ground and nailed to wooden corner posts. To prevent beetles from escaping by climbing out, a smooth plastic lip facing downwards was stapled to the inside top edges of the walls. Wall crevices were sealed with rubber cement. Vegetation in the enclosure was clipped and removed. Twenty-four smooth white plastic trays, 15 x 5 cm and 4 cm deep, were inserted into the ground, in three rows of eight. Trays were about 25 cm apart. Plastic plates, 16 x 10 cm with a 3 cm wide slot extended lengthwise in the center and with lips facing downward were placed over the trays. These allowed the beetles to slide into the trays without clinging to the rims, as well as prevented them from leaving the traps. To ensure that covering plates were flush with the ground, smoothed mud was tightly applied around the edges. Dead leaves were sprinkled over the ground to provide shelters. A photograph of the enclosure is shown in Figure 10.

On August 7 (1980), 50 individuals of each *A. nigriceps*, *A. ferruginosum* and *A. thoreyi*, freshly collected in the morning (at Lake 6 and Field 4) were released into the enclosure at 1245h (Standard Time). Traps were then checked at two-hour intervals starting at 1500h (ST). Beetles in the traps, as well as those seen walking on the enclosure walls, were captured with a mouth aspirator, tallied, and released immediately into the enclosure among dead leaves. Recordings were pursued until the next day at 1500h.

On August 7, the weather was cloudy during the first half of the day. There was a brief shower in the early afternoon, but the sky cleared afterward and the sun shone. It was sunny on August 8. The maximum temperature was 21°C

Figure 10. Field enclosure used to study daily activity.



on both days, and the nightly minimum was 2°C.

3.2.5 Wing morphs of *A. nigriceps* and *A. ferruginosum*

In order to obtain estimates of the relative proportions of macropters and brachypters in populations of *A. nigriceps* in the study area, a series of marshes was surveyed in mid-summer 1980. Wing condition of *A. nigriceps* individuals is easily assessed because the elytra are translucent. In macropters, the reflexed hind wings are seen through the elytra, whereas in brachypters, only the abdominal segments are visible.

Thirteen sites were visited between June 17 and July 21, 1980. These are listed in Appendix I, and ten of them are mapped in Figure 1. Sites located outside the map are (1) "Busby", *ca.* 53°57′N – 113°54′W, situated a few meters west of Busby, (2) "East Alexander", *ca.* 53°48′N – 113°54′W, situated at the east entrance of Alexander Indian Reserve 134, and (3) "West Morinville", *ca.* 53°47′N, – 113°40′W, adjacent to highway 2, west of Morinville. Unmapped sites are located within a distance of at most 20 km of the area shown in Fig. 1.

At each site, approximately 40 specimens of each sex were collected, tallied for wing condition and released. In addition to data from the sites mentioned above, sampling results from Lake 1 and Lake 2 and from Barrhead obtained between mid-June and mid-July were used as comparable data sets.

For *A. ferruginosum*, wing condition was checked on about 100 specimens collected at Lake 5, Lake 7, Field 1, Field 2 and Field 3 during 1979 and preserved in 70% ethanol. Females collected during 1980 for ovary condition were also checked for wing condition.

3.3 Results

3.3.1 Adult population dynamics

Figures 11 and 12 illustrate the overwintered and teneral adult population curves for the dominant *Agonum* species at George Lake and Barrhead respectively, for all pooled macrohabitat counts. No curve is presented for *A. lutulentum* at George Lake because of the small number of specimens sampled (see Table 3, Chapter 2). Relatively large sampling errors, probably a combined effect of small sample sizes and of patchy distribution of the beetles, tend to blur the patterns. Nevertheless, some worthwhile considerations can be drawn about trends.

The data show that all species were present at or near maximum seasonal densities at the beginning of the sampling period in mid-May. All species were encountered throughout the season and separate peaks of abundance of overwintered adults did not occur for each species.

Overwintered adult densities of *A. ferruginosum*, *A. thoreyi* (Figs. 11 and 12) and *A. lutulentum* (Fig. 12) decreased very gradually from mid-June onward. This suggests that mortality rates of overwintered adults of these species were low, and that overall mortality spanned most of the second half of the summer. The decline was more marked at Barrhead, where the number of overwintered adults approached or declined to zero for *A. thoreyi* and *A. lutulentum*. The abundance pattern for *A. nigriceps* was more irregular than

Figure 11. Overwintered and teneral adult population curves for species of marsh *Agonum* at George Lake during 1980. (Means ± 1 SE).

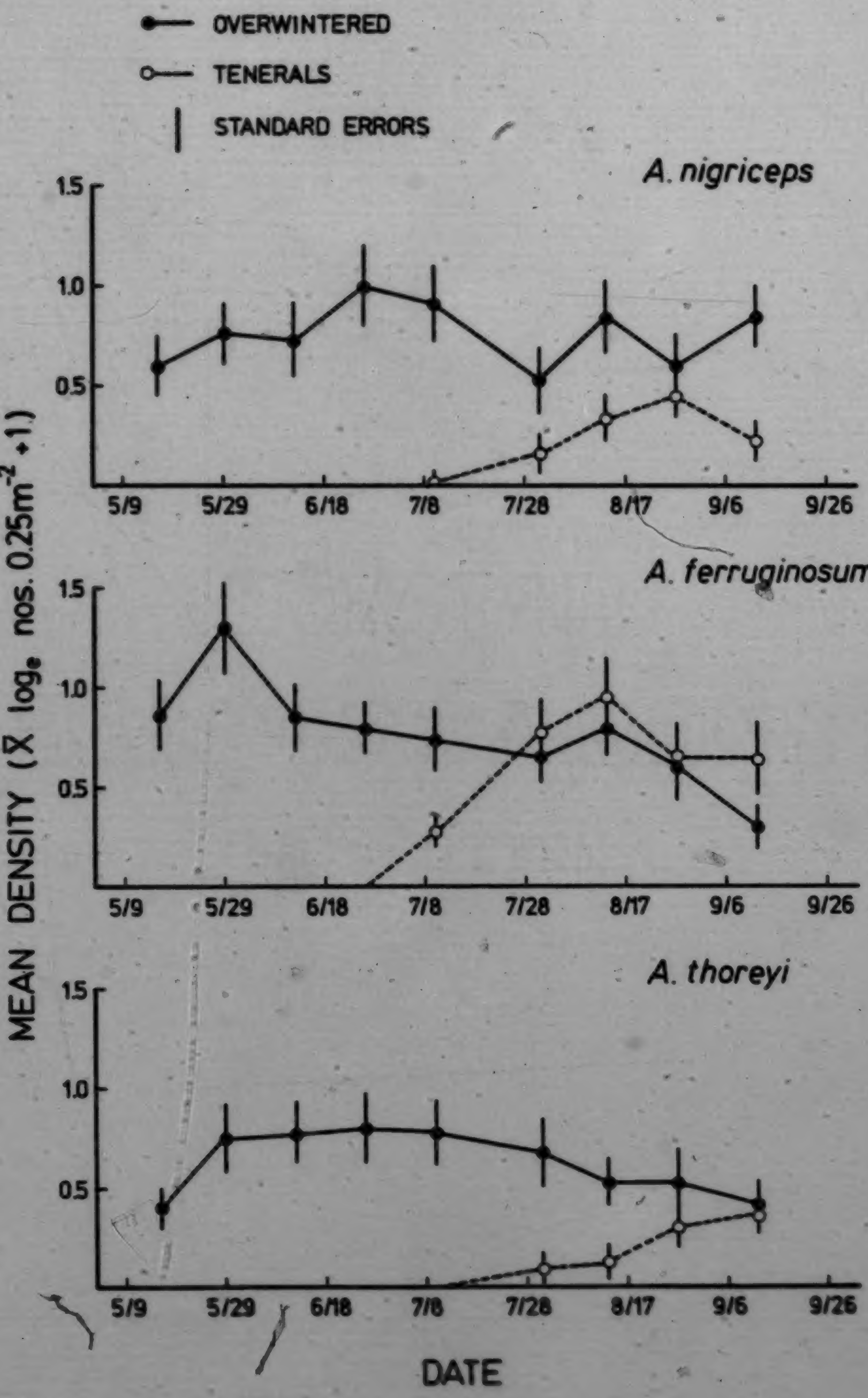
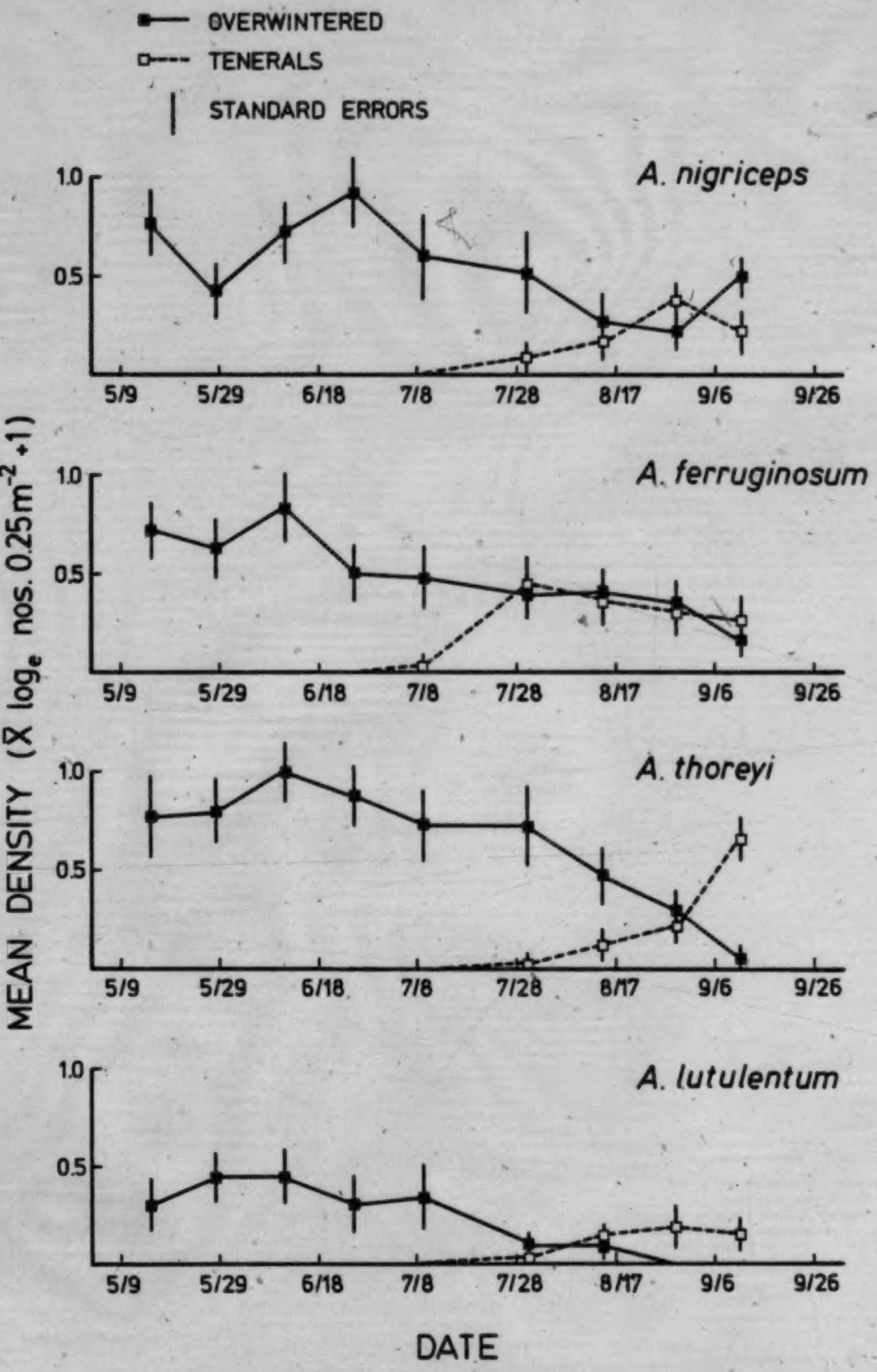

OVERWINTERED
TENERALS
STANDARD ERRORS
A. nigriceps
A. ferruginosum
A. thoreyi
MEAN DENSITY ($\bar{X}$ log$_e$ nos. 0.25m^{-2} +1)
1.5
1.0
0.5
5/9
5/29
6/18
7/8
7/28
8/17
9/6
9/26
DATE

Figure 12. Overwintered and teneral adult population curves for species of marsh *Agonum* at Barrhead during 1980. (Means ± 1 SE).

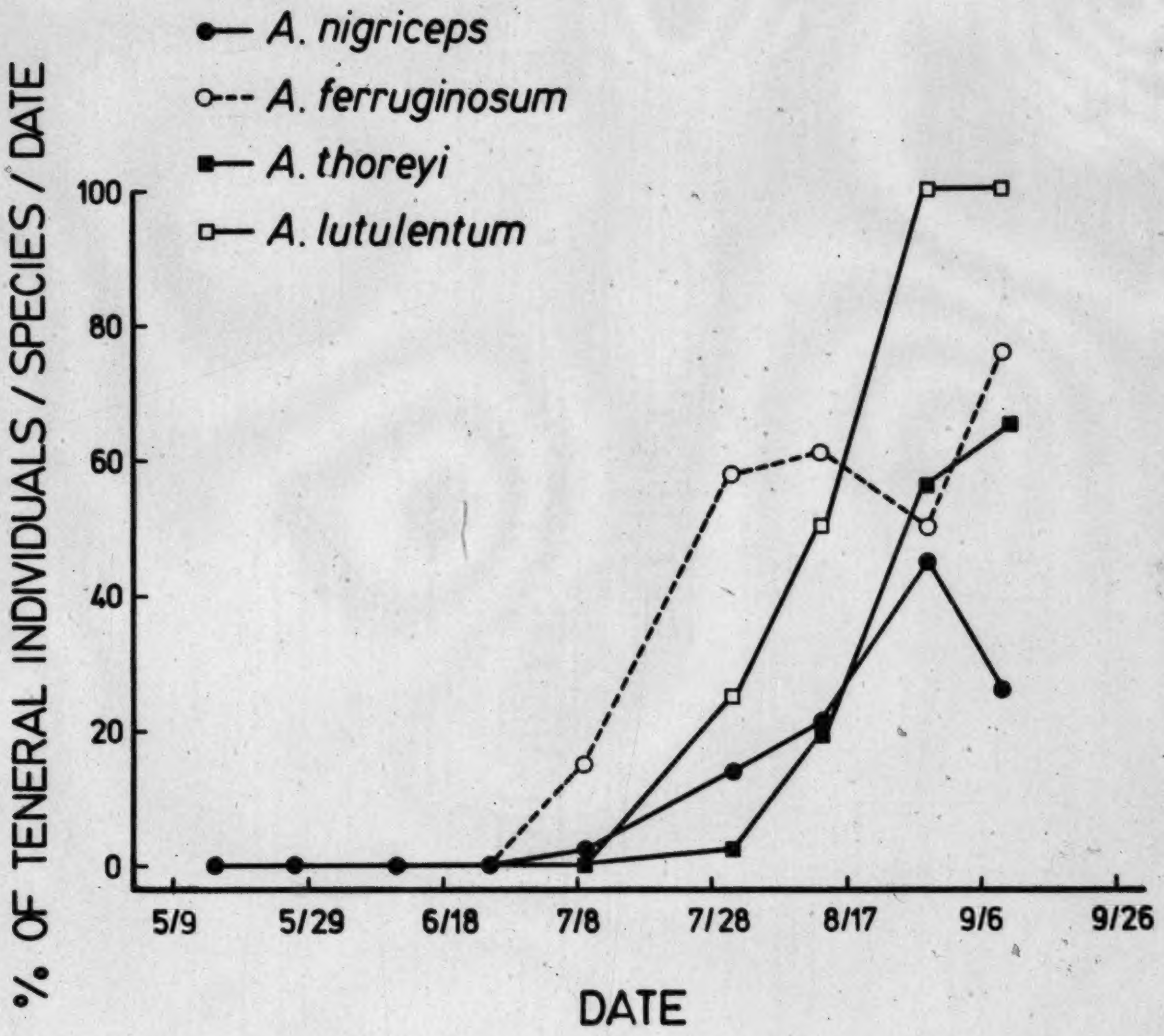

OVERWINTERED
TENERALS
STANDARD ERRORS
A. nigriceps
A. ferruginosum
A. thoreyi
A. lutulentum
1.0
0.5
5/9
5/29
6/18
7/8
7/28
8/17
9/6
9/26
MEAN DENSITY ($\bar{X}$ log$_e$ nos. 0.25m^{-2} +1)
DATE

that of the other species and did not reveal a tendency to gradual decline at either site. In the early fall, *A. nigriceps* populations were still almost at levels comparable to those of late spring, suggesting very low summer mortality in overwintered adults of this species.

Both generations of overwintered and summer adults widely overlapped in time for all species except *A. lutulentum*, resulting in no significant dip in the overall population during the summer season. Some temporal separation between the two generations of adults is suggested for *A. lutulentum* only (Fig. 12).

Teneral adults began to appear in July, and contrasting with the parent generation, they showed interspecific differences in peaks of abundance. Tenerals of *A. ferruginosum* began to appear in early July and had already reached a maximum by early August, while tenerals of the other species emerged later in July and did not peak until late August. These differences are better appreciated in Figure 13, where the abundance of teneral adults is expressed as a percentage of the total catch of each date for each species (data from both sites pooled). The bulge of emergence of *A. lutulentum* tenerals occurred between that of *A. ferruginosum* and that of *A. nigriceps-A. thoreyi* tenerals. Slopes of the curves indicate relatively fast and about equal rates of emergence for *A. ferruginosum*, *A. thoreyi* and *A. lutulentum*, but a slower rate for *A. nigriceps*. The drop in relative abundance of tenerals of *A.*

Figure 13. Abundance curves for teneral adults for species of marsh *Agonum* during 1980.


●— A. nigriceps
○--- A. ferruginosum
■— A. thoreyi
□— A. lutulentum
100
80
60
40
20
0
% OF TENERAL INDIVIDUALS / SPECIES / DATE
5/9
5/29
6/18
7/8
7/28
8/17
9/6
9/26
DATE

nigriceps in September is probably spurious owing to the fact that tenerals of this species were increasingly difficult to separate from old adults in the field as the season progressed.

3.3.2 Teneral emergence sites

Table 4 shows the proportions of teneral adults found in the various macrohabitat categories of the two study sites. Teneral peaks of *A. nigriceps* occurred in sedge tussocks at both marshes. *A. ferruginosum* and *A. thoreyi* tenerals were most abundant in floating cattails at George Lake, but at Barrhead peaked in flooded and in unflooded sedge meadow respectively. The teneral peak for *A. lutulentum* was in the flooded sedge meadow. Inasmuch as distribution of tenerals can indicate place of breeding and larval habitat, the data of Table 4 suggest that the species generally bred and developed in the macrohabitat in which they were most abundant (compare with Figs. 5 and 6 of Chapter 2). Exceptions to this pattern are *A. thoreyi* and *A. lutulentum* at Barrhead, which showed highs in the sedge tussocks with respect to overall abundance but not with respect to teneral abundance.

3.3.3 Ovary condition and reproductive effort

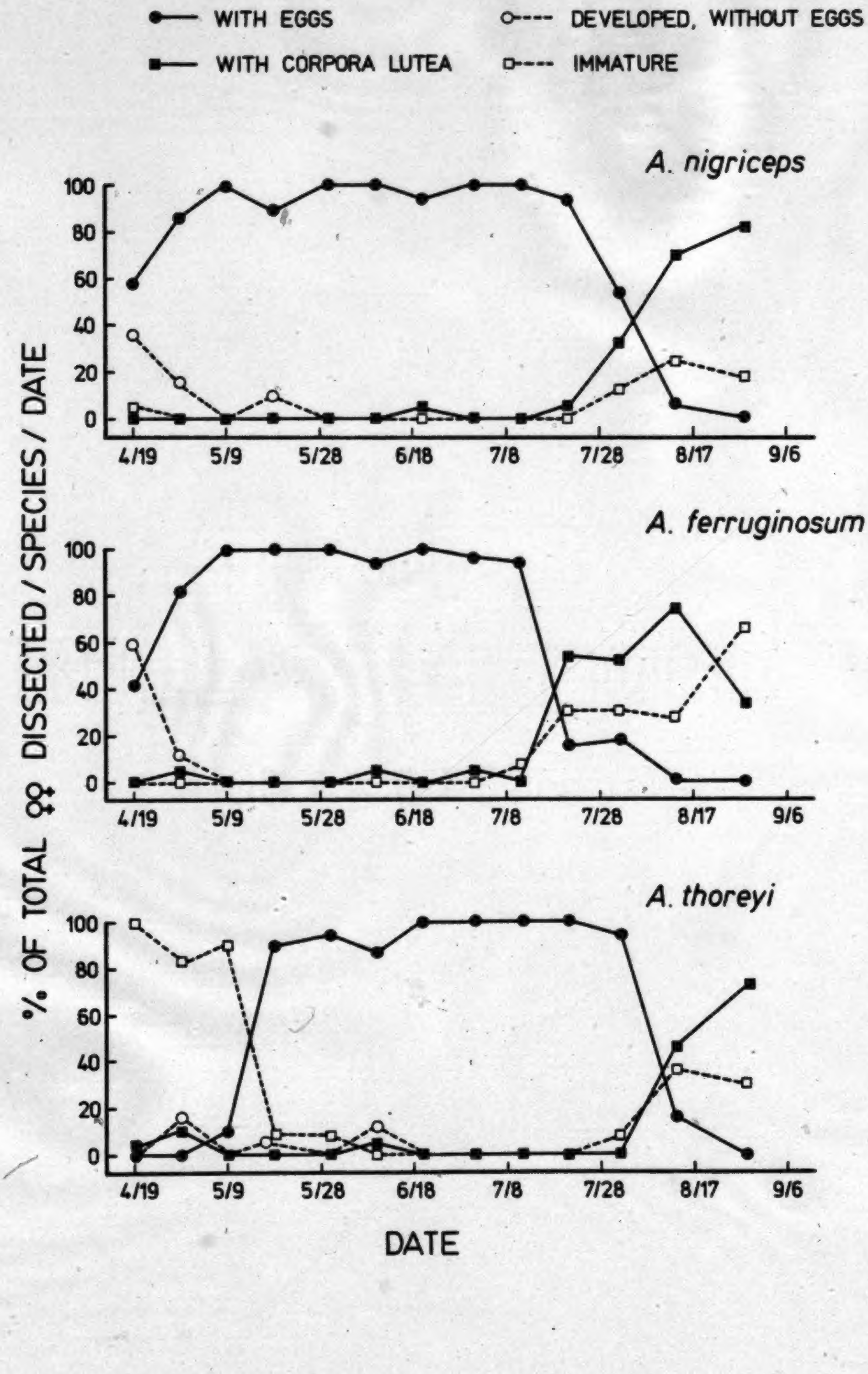
Figure 14 depicts the seasonal changes in relative proportions of the four types of ovary conditions observed during 1980. These data are based on dissection of 785

TABLE 4

Percentages of teneral *Agonum* from various macrohabitat categories at the two main study sites

MACROHABITAT	SPECIES OF *Agonum*			
	nigriceps	*ferruginosum*	*thoreyi*	*lutulentum*
GEORGE LAKE				
wet forest margin	0	0	8.9	--
unflooded sedge meadow	15.2	2.8	15.6	--
flooded sedge meadow	6.5	11.1	17.8	--
sedge tussocks	47.8	18.3	13.3	--
floating cattails	30.4	67.9	44.4	--
N	46	252	45	--
BARRHEAD				
unflooded sedge meadow	0	12.1	40.9	0
flooded sedge meadow	9.7	65.5	20.5	41.2
sedge tussocks	54.8	5.2	22.7	29.4
floating cattails	35.5	17.2	15.9	29.4
N	31	58	44	17

Figure 14. Seasonal distribution of ovary conditions in females of marsh *Agonum* species during 1980.


WITH EGGS
DEVELOPED, WITHOUT EGGS
WITH CORPORA LUTEA
IMMATURE
A. nigriceps
A. ferruginosum
A. thoreyi
% OF TOTAL ♀♀ DISSECTED / SPECIES / DATE
100
80
60
40
20
0
4/19
5/9
5/28
6/18
7/8
7/28
8/17
9/6
DATE

females. All females of *A. nigriceps* and *A. ferruginosum* were already in breeding condition by mid-April (i.e. at least with developing ovocytes) and about half had mature eggs and were possibly ovipositing. Full breeding condition was rapidly attained afterward, as by early May all females of these two species contained ripe eggs.

In contrast, females of *A. thoreyi* had still immature ovaries in early spring. In fact, on April 19, the first date of collecting of females, no individuals of *A. thoreyi* could be found in the marsh, while there were plenty of the other two species. During several hours of collecting, only 5 males and 3 females of *A. thoreyi* were found in the forest litter bordering Lake 5 site. This suggests that *A. thoreyi* left overwintering quarters later than *A. nigriceps* and *A. ferruginosum*. Breeding condition did not appear until the second week of May. At that time however, full breeding condition was attained very abruptly within about ten days. Thus the breeding period of *A. thoreyi* differed from that of *A. nigriceps* and *A. ferruginosum* by about a full month.

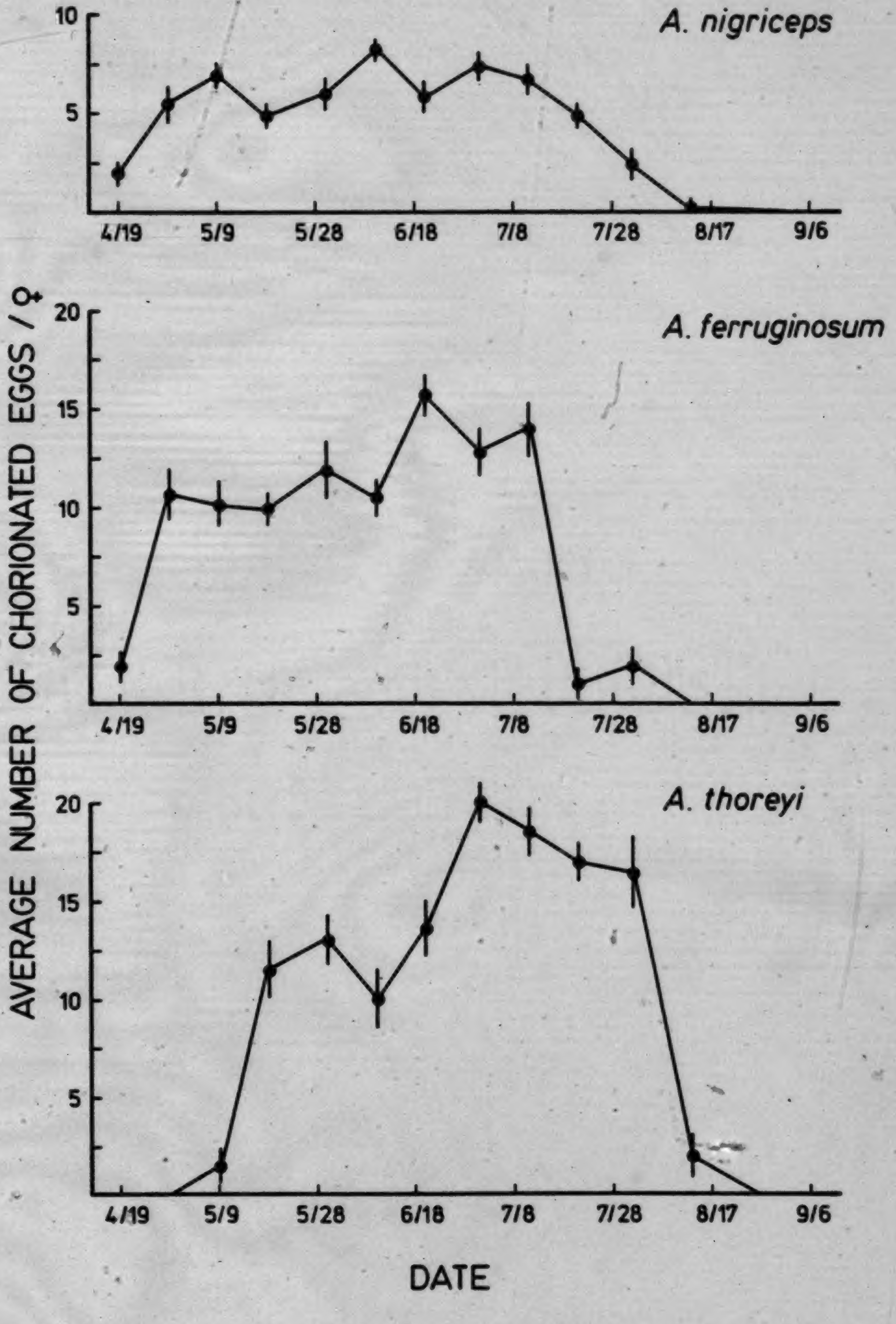
Spring females with ovaries containing corpora lutea are individuals that reproduced during the preceding summer and survived a second winter (Gilbert, 1956). Very few such females were found in the spring (Fig. 14): about 10% of spring females of *A. thoreyi*, fewer than 3% for *A. ferruginosum* and none for *A. nigriceps*. Their very low occurrence suggests low survival of old individuals through a second winter.

Full breeding condition spanned a considerable portion of the summer in all species, and ended abruptly for *A. ferruginosum* and *A. thoreyi*. The decline of gravid females was more gradual for *A. nigriceps*.

The seasonal reproductive effort of each species, estimated by average numbers of eggs per female, is shown in Figure 15. Egg production climbed quickly in all species and remained high for a period of about four months. For *A. ferruginosum* and *A. thoreyi* however, there were second bursts in egg production in the middle of the reproductive period; this was especially marked for *A. thoreyi*. Egg production gradually declined for *A. nigriceps*, slightly preceding the diminution of the number of egg-carrying females (compare with Fig. 14), but dropped sharply for the other species, simultaneously with the number of egg-carrying females.

Egg production differed among species. *A. nigriceps* females had significantly fewer eggs than the other at any comparable point in their breeding period. A maximum average of about 8 eggs per female was reached for *A. nigriceps*, as compared to 16 and 20 eggs for *A. ferruginosum* and *A. thoreyi* respectively. Thus species differed both in timing of breeding period and in magnitude of reproductive effort (fertility).

Figure 15. Seasonal distribution of reproductive effort of marsh *Agonum* species during 1980. (Means ± 1 SE).


A. nigriceps
10
5
4/19
5/9
5/28
6/18
7/8
7/28
8/17
9/6
A. ferruginosum
20
15
10
5
4/19
5/9
5/28
6/18
7/8
7/28
8/17
9/6
A. thoreyi
20
15
10
5
4/19
5/9
5/28
6/18
7/8
7/28
8/17
9/6
AVERAGE NUMBER OF CHORIONATED EGGS / ♀
DATE

3.3.4 Developmental time

Tentative estimates of field developmental times were obtained by counting the number of days that elapsed between the date at which 50% of the dissected females had ripe eggs and that at which 50% of sampled adults were tenerals. The results, shown in Table 5, suggest that *A. ferruginosum* and *A. thoreyi* had quite similar developmental times but that *A. nigriceps* developed much more slowly.

3.3.5 Daily activity

Results of the enclosure experiment for measuring daily locomotory activity, expressed as percentages of the total species catches, are presented in Figure 16. Active beetles appeared after sunset. Activity peaked quickly around midnight, then decreased more or less gradually to cease at sunrise. Thus all three species were nocturnal, and did not exhibit significant temporal segregation on the daily scale.

3.3.6 Regional distribution of wing dimorphic *Agonum*

Among the dominant species of *Agonum* of the study area, significant wing dimorphism was exhibited only by *A. nigriceps*. In this species, high proportions of brachypters were found in several populations.

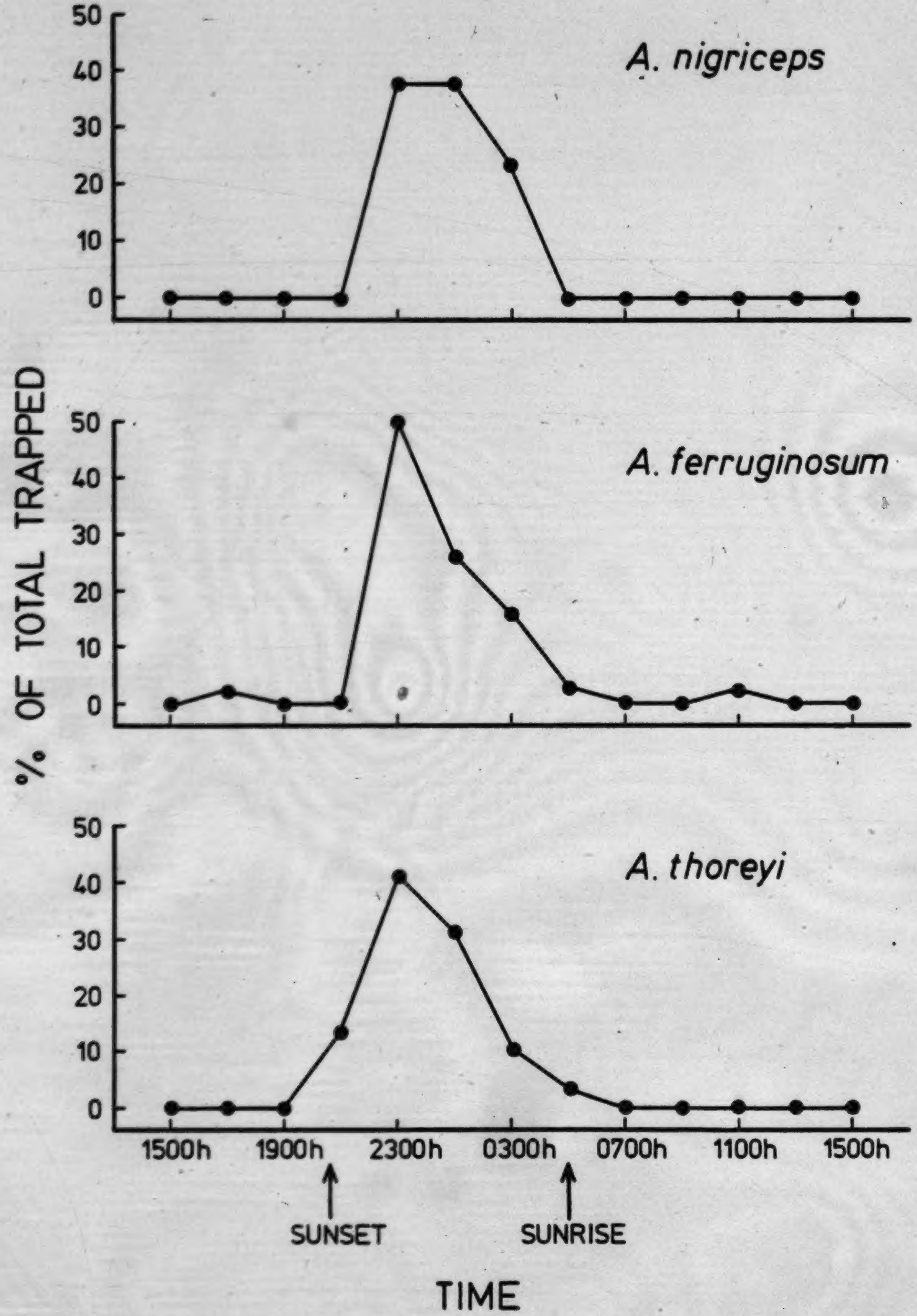
Relative percentages contributed by each morph are presented in Table 6 for all marshes surveyed. The data indicate wide marsh to marsh variation in the proportions of each morph, ranging from no macropters (Nakamun 1) to almost

TABLE 5

Time relation between female egg production and teneral emergence in 1980

SPECIES	DATE		DAYS ELAPSED
	≥50% OF ♀♀ WITH EGGS	≥50% TENERALS	
A. nigriceps	April 19	August 29	134
A. ferruginosum	April 29	July 31	95
A. thoreyi	May 19	August 29	102

Figure 16. Daily locomotory activity of species of marsh *Agonum* in an experimental field enclosure.



A. nigriceps
A. ferruginosum
A. thoreyi
% OF TOTAL TRAPPED
50
40
30
20
10
0
1500h
1900h
2300h
0300h
0700h
1100h
1500h
SUNSET
SUNRISE
TIME

TABLE 6

Distribution (%) of wing morphs of *Agonum nigriceps* in various marshes (mid-summer 1980)

MARSH	% MACROPTERS	% BRACHYPTERS	TOTAL N
Field 1	11.8	88.2	85
Field 2	18.5	81.5	81
Field 4	10.7	89.3	84
Road South 1	16.9	83.1	83
Road South Big	4.8	95.2	83
Busby	17.6	82.4	85
East Alexander	33.3	66.7	84
West Morinville	45.9	54.1	85
Barrhead	25.3	74.7	163
Barrhead Yoder	17.0	83.0	88
Nakamun 1	0	100.0	18
La Nonne 1	2.4	97.6	83
La Nonne 2	13.6	86.4	81
Lake 1+2	32.1	67.9	182
Lake 7	51.7	48.3	87

$X^2=147.30$, df=14, $p<.001$

52% macropters (Lake 7). Heterogeneity was highly significant as indicated by the chi-square value calculated across marshes. Differences were observed even between sites located around George Lake (Lake 1+2 and Lake 7). Brachypters were more abundant at all sites except at Lake 7, where macropters were as common as brachypters.

The relative proportions of brachypters and macropters were statistically similar for both sexes, as indicated by the results of chi-square tests performed for each marsh (Table 7). The only exception to this pattern is Lake 1+2, where there were about 13% fewer macropters among females. Results from Nakamun 1, though showing a difference between sexes, cannot be given too much confidence since only 18 individuals could be collected (in two hours searching).

Despite significant numbers of macropters in the region, only one flight record is available for *A. nigriceps*, observed on a sunny spring afternoon at a small woodland pond near the George Lake field station (May 14, 1981)[1].

For *A. ferruginosum*, only 6 brachypters were found out of 100 individuals checked in 1979, and all were from the George Lake cattails. Specimens from other marshes (Field 1, Field 2, Field 3, Busby) were all long-winged. No brachypters were found among the 255 specimens checked in 1980. Individuals brought back to the laboratory frequently flew off to the windows in day light if they were in open

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[1] I am indebted to J.D. Fournier for this observation.

TABLE 7

Chi-square values for test of independence
of wing morphs of *A. nigriceps* with respect to sexes
in various marshes (mid-summer 1980)

MARSH	BRACHYPTERS		X^2*	p
	% ♂♂	% ♀♀		
Field 1	46.7	53.3	0.039	.843
Field 2	51.5	48.5	0.648	.421
Field 4	49.3	50.7	0.124	.724
Road South 1	53.6	46.4	4.832	.028
Road South Big	50.6	49.4	1.001	.317
Busby	54.3	45.7	2.169	.141
East Alexander	46.4	53.6	0.857	.355
West Morinville	47.8	52.2	0.101	.751
Barrhead	52.1	47.9	1.016	>.100
Barrhead Yoder	49.3	50.7	0.035	.852
Nakamun 1	61.1	38.9	-**	---
La Nonne 1	50.6	49.4	<0.001	.986
La Nonne 2	47.1	52.9	0.209	.648
Lake 1+2	43.9	56.1	7.864	<.010
Lake 7	57.1	42.9	1.401	.237

* with 1 degree of freedom
** cannot be computed (n of macropters=0)

trays. A few beetles were also observed flying and landing on sedge and cattail plants, in the afternoon sunshine in mid-June. Unfortunately, no exact record of the dates was made.

3.4 Discussion

3.4.1 Adult mortality

Several workers have provided evidence showing that mortality of adult carabids is higher during the breeding season than at other times of the year (Schjøtz-Christensen, 1965; Murdoch, 1966a; Luff, 1973; Grüm, 1975). In spring breeders, a typical mortality pattern produces a decline in overall population abundance in the middle of the summer (e.g. Barlow, 1970; Goulet, 1974; Bousquet and Pilon, 1977), caused by a delay between the decline of overwintered adults and the emergence of offspring. The present findings contrast with such a pattern, suggesting only a slow decline in adult populations of dominant marsh *Agonum* during the breeding season. In *A. nigriceps*, the summer mortality seemed insignificant. Low adult mortality during the breeding period coupled with low occurrence of two-year old females in the spring suggests that either autumn mortality (owing to senescence) or winter mortality is high. In the present situation, the former alternative seems more likely because winter mortality in marsh *Agonum* is generally very low (Murdoch, 1966a; Wasner, 1979).

Murdoch (1966a) has expressed the possibility, supported by some evidence, that the high mortality of the breeding season might largely be attributed to predation by small insectivorous mammals. The *Agonum* populations studied by Murdoch occurred in unflooded marshes. In flooded habitats such as in the present study, it is possible that predation by insectivorous mammals is depressed because these predators may face reduced searching efficiency in heterogeneous vegetation. This might help explain the relatively high survival of adults during the summer.

High summer survival of adults may have marked populational consequences: as more adults participate longer in the collective reproductive effort, populations may grow larger. Thus increased adult survival may also be implicated in high densities of flooded marsh populations.

3.4.2 Timing differences and life history adaptations

No significant differences in timing of adult activity were observed either over the season or on the daily scale. Complete overlap in daily activity is consistent with the results of other studies on closely related species (Paarmann, 1966; Goulet, 1974; Spence, 1979a).

As regards seasonal timing, it must be noted that the population curves are truncated at both ends because the activity season for these species started and ended before sampling was commenced and terminated. However early spring collection of females suggests a later onset of activity in *A. thoreyi*. This apparently led to a timing difference of almost a month between the beginning of the breeding period of this species and that of *A. ferruginosum* and *A. nigriceps*. Other workers have observed similar delays in the reproductive period of *A. thoreyi* relative to other marsh

Agonum in various parts of Europe (Dawson, 1965; Greenslade, 1965; Wasner, 1979). This may be related to a higher temperature threshold for activity and gonad development.

The implications for coexistence of differences in breeding time may be at the larval stage. Carabid larvae are notorious for their aggressiveness and will readily attack other larvae of a manageable size, even their conspecifics. Thus in dense populations such as in the marsh, simultaneous hatching peaks of several species might result in a high level of interspecific predation (added to possible cannibalism). If such situations occurred, they might be more detrimental to the small sized species because their larvae would be disavantaged in encounters with larvae of a larger species (high adult densities coupled with high egg production suggest high larval densities, thus making such encounters very likely)[2], and would perhaps suffer heavier losses by being wounded or eaten.

However a small species may bridge the size gap by breeding early: if its larvae hatch out earlier than those of larger species, they could grow to a sufficient size to later withstand confrontations in encounters with larvae of larger species when the latter begin to emerge. A time difference of only a few weeks would be sufficient. Intraspecific interactions would not be precluded in that way, but the total of both inter- and intraspecific interactions for a species would be reduced.

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[2] Low numbers of larvae sampled during this study resulted from their difficult extraction, and certainly not from low densities.

In the guild under consideration, *A. nigriceps* is the smallest species; *A. ferruginosum* is intermediate in size and *A. thoreyi* is the largest (see Chapter 5). As was shown, the two former species breed earlier than *A. thoreyi*. Thus it is possible that the discrepancy in reproduction represents an adaptation that helps the smaller species to coexist with the larger one by minimizing detrimental effects of aggressive interactions by larvae. This pattern might have greater importance for *A. ferruginosum* which showed greatest habitat and microhabitat overlap with *A. thoreyi*.

The above mechanism may easily evolve and be maintained by selection at the individual level. If early hatching and development are linked to greater chances of survival, eggs and larvae with slightly lower development and/or growth threshold will be selected for, thus gradually leading to a shift towards early breeding in a population. An empirical test of that hypothesis could be provided by examining breeding times in areas of allopatry for the species concerned.

It might be argued that *A. nigriceps* begins to breed earlier than the other species because of an apparently lower rate of development: early breeding would enhance the chances for a significant portion of its offspring population to complete development and reach the adult stage before cool autumn temperatures and early cold spells. This scheme seems less likely for *A. ferruginosum* which apparently completes its development rapidly, with the bulk of tenerals already emerging in mid-summer. It is possible that early breeding time is primarily governed by duration of the developmental programme in *A. nigriceps* while being maintained by interspecific interactions in *A. ferruginosum*. The data do not allow me to discriminate between these hypotheses.

The seemingly lengthy development of *A. nigriceps* may be related to the tendency for this species to occur in structurally simple microhabitats (Chapter 2). In these sites, it is likely that the overall abundance of food is lower than in, for example, dense patches of dead plant. Individuals spending a significant portion of their time in patches of habitat of low productivity would see their development lengthened.

Reproductive efforts of all species occupied a long period of the summer and were remarkably high in both *A. ferruginosum* and *A. thoreyi*. Wasner (1979) reported similarly high fertility for *A. thoreyi* populations of southwest Germany and hypothesized that this, coupled with the prolonged egg production phase, could correspond to a form of spreading of risk [in Boer's (1968) sense] in time. The present data are consistent with this interpretation. However, more factors are likely to be implicated, because eggs laid late in the summer probably never complete development to the adult stage before the winter. Murdoch

(1966a) has suggested that food shortage may occasionally occur among marsh *Agonum* populations. Differences in food availability may explain dramatic yearly variations in fertility observed by that author and by Wasner (1979) in *A. fuliginosum* and *A. thoreyi* respectively. The high reproductive efforts observed here for *A. ferruginosum* and *A. thoreyi* might thus reflect a great abundance of food items, suggesting that these species might be r-selected. On the other hand, the long developmental time, low summer mortality of adults and relatively low fertility of *A. nigriceps* suggest a K-selected species. Wasner (1979) suggested that further investigation on the mechanisms of coexistence among sympatric *Europhilus* might well begin by exploring such differences in life history adaptations. Evidence from the present study also points in that direction.

Wasner (1979) has proposed that timing differences explain the microsympatry of four species of *Europhilus* in West Germany. In a similar fashion, the dominant *Europhilus* species of the George Lake area afford some partitioning along the temporal niche axis.which may account, at least in part, for their coexistence.

3.4.3 Wing dimorphism and marsh colonization

Lindroth (1949: 335ff; 1979) has elegantly discussed how geographical variation in the relative frequencies of macropters and brachypters of several Nearctic and

Palearctic carabid species can be related to the post-glacial expansion of their range from glacial refugia. In these species, populations in the glacial refugium area are entirely brachypterous, and the proportion of macropters increases as one moves away from the refuge region. Such explanation accounts for broad patterns of wing dimorphism. They seem corroborated by historically more recent range expansions of carabids into newly formed habitats (Dutch polders), spear-headed by entirely macropterous populations (Meijer, 1974).

This may lead one to suppose that variations in the relative frequencies of wing morphs within a small region are insignificant. However there seems to be no work that documents patterns of wing dimorphism from a regional perspective, particularly in relation to the distribution of habitats.

3.4.3.1 Wing dimorphism in *A. nigriceps*

The present survey of wing dimorphism in *A. nigriceps* revealed startling variations in the wing morph ratio on the regional scale. Far from invalidating previous range expansion hypotheses, these results imply that once a species has a widespread distribution (*A. nigriceps* is transamerican), local factors may come into play to affect the relative frequencies of wing morphs.

Marshes are patchy habitats which may afford various degrees of permanence depending upon the extent to which they are affected by periodic droughts, such as occur in central Alberta (e.g. during the spring of 1980). The maintenance of macropters in regional populations may thus be favoured through the recolonization of periodically depauperated marshes. The proportion of macropters in a given marsh at a given time may result from a combination of factors including degree of permanence of the marsh, its age, distance to other surrounding marshes, its relative isolation by woodland patches as well as relative duration of drought intervals. The discrepancies in morph frequencies observed at different sites around George Lake are compatible with such a scheme, as they may depend on how recently a section of the lake edge has grown marsh vegetation and how distant it is from other marshy sections around the lake.

The relatively recent -less than two hundred years- opening of large patches of woodland into open farmland might have had a significant impact on the regional pattern of wing morph distributions in the study area, by favouring the multiplication of marshes habitable by *A. nigriceps*, reducing the isolation effect provided by woodland and perhaps enhancing drought effects through alteration of the local climate. Thus the present pattern of wing dimorphism might have partly been induced by artificial and accelerated alteration of the environment by man.

At present no detailed explanation can be given for the observed regional pattern of wing dimorphism in *A.*

nigriceps, because the data are too limited in space and time. Attempts to explain the pattern can constitute an extensive study . The problem could be approached by viewing each marsh as a terrestrial "island", thus providing fascinating opportunities to test, both empirically and experimentally, predictions of the theory of island biogeography (MacArthur and Wilson, 1967). Field work might begin by searching an undisturbed forested area with marshes harbouring populations of *A. nigriceps* (for example in northern Alberta) and comparing wing morph frequencies with those of the George Lake area.

3.4.3.2 Wing dimorphism in *A. ferruginosum*

Known distribution records (Lindroth, 1966: 589) suggest that *A. ferruginosum* has a more southern distribution than *A. nigriceps*, with a northern limit in central Alberta. The almost entirely macropterous populations of *A. ferruginosum* in the study area may indicate a relatively recent invasion of the region. A northward expansion of the distributional range of *A. ferruginosum* could have been driven by the opening of woodland in northcentral Alberta, which undoubtedly created a myriad of new marsh habitats.

4. EXPERIMENTAL ANALYSIS OF CLIMBING BEHAVIOR

4.1 Introduction

An early observation in this study was that individuals of *A. nigriceps* regularly climbed and remained resting on the narrow rims of laboratory containers in which they were kept. Individuals of *A. ferruginosum* and of *A. thoreyi* also showed this behavior, but to a less pronounced degree. This was not observed in other species of *Agonum* and of carabids kept in similar conditions.

Even though some carabids confined to the laboratory display aberrant reactions (e.g. Landry and Chamberland, 1976) possibly in response to discomfort or stress, this did not appear to be so for the present set of observations. The climbers, especially *Agonum*, seemed to look for narrow, elevated places and for vertical surfaces, instead of hiding under shelter leaves as adults of most other species did. It appeared likely that this unusual behavior could be related to structure of the habitat in which these marsh *Agonum* occurred, namely flooded vegetation. The idea was that if members of a species spent a major part of their active life among the vegetation of inundated marshes, they might have a preference for foraging and resting on narrow, more or less vertical surfaces, such as provided by, for instance, sedge and cattail plants.

In this chapter, I compare experimentally the frequency at which individuals of various species of marsh *Agonum* use vertical surfaces, and assess the possibility that differences in climbing behavior may help account for differences in habitats occupied.

4.2 Material and methods

4.2.1 Species tested and hypothesis

Central to the tests were the main dwellers of inundated marshes, *A. nigriceps*, *A. ferruginosum* and *A. thoreyi*. Adults of these species were tested in all experiments. *A. lutulentum* was included only in the last experiment. Other *Agonum* inhabiting the unflooded portion of marshes were also included for comparison. They were: *A. gratiosum*, *A. sordens*, *A. superioris*, *A. affine*, *A. propinquum*, *A. anchomenoides* and *A. mannerheimi*.

Adults of a species were given the opportunity to climb and stay on narrow vertical structures mimicking plants. It was hypothesized that the propensity for climbing should be highest among flooded marsh species, in connection with use of the vegetation as a foraging and resting place, and less pronounced or absent in species mainly occupying unflooded portions of marshes because of more common foraging on the ground. "Controls", i.e. adults of species known as genuine epigaeic beetles inhabiting habitats never inundated were included in the experiments. They were *A. cupreum*, a dry field inhabitant, active on the ground, and *A. retractum*, a woodland dweller living in the soil litter and among dead leaves.

4.2.2 Apparatus and laboratory conditions

Three similar experiments were performed during three summers (1978 - 1980). Beetles used in the experiments were collected at various sites in the study area.

In all three experiments, 600 ml pyrex beakers were employed as experimental arenas in which horizontal and vertical structures were set (see below). Beakers were covered with sheets of paraffin to prevent beetles from escaping and to maintain an adequate moisture level. A photograph of an experimental beaker is shown in Figure 17.

Experiment 1 (1978). Ten disks of filter paper of a diameter equal to that of the beakers were stacked on the bottom of each beaker to serve as horizontal substrate. The disks fitted tightly to the beakers' sides to prevent carabids from crawling beneath and remaining there (thigmotactic reaction) thereby biasing the results. Ten blunt toothpicks were inserted into the paper layers to serve as vertical structures; five of them had the top half bent. The paper substrate was moistened with distilled water.

Experiment 2 (1979). A 1 cm thick layer of moist mud collected at a marsh edge was evenly applied on the bottom of each beaker to serve as horizontal substrate. Six 10 cm pieces of *Carex rostrata* stem (with leaves removed) were inserted into the substrate as vertical structures. Hollow stems were plugged at their tip with pieces of twigs.

Figure 17. A beaker with mud substrate and sedge straws used for climbing experiment.

400
300
200
100

Experiment 3 (1980). The setting was as in experiment 2.

Beakers were arrayed in an incubator at constant temperature and with a 24-hour light-dark regime. Photoperiods were comparable to duration of natural days at the time beetles were collected and the experiments performed. Informations on incubator settings and dates for all experiments are provided in Appendix IV. Conditions differed slightly among experiments because different incubators had to be used each time.

4.2.3 Experimental procedure

Groups of 10 beetles of the same species were introduced into the beakers. Four beakers were set for each species in experiment 1, while sets of two were prepared in experiments 2 and 3. The beetles were provided with plenty of food (freeze-killed vestigial-winged *Drosophila*) for the duration of the experiment. They were left for a few days to become habituated to the artificial environment. Following the habituation period, the number of beetles on the vertical structures was recorded periodically. In experiment 1, observations were made twice a day, once during light time and once during dark time. In experiments 2 and 3, several recordings a day were made both during photophase and scotophase. Recordings were separated by at least one hour, starting one hour after and ending one hour before light-dark changes. Scotophase recordings were done with a head lamp covered with a red photographic filter (Nikkor R60, Nippon Kogabu K.K., Tokyo, Japan) and with layers of paper tissue; the covered lamp light intensity was 0.1 lux. After a recording, beakers were briefly shaken to allow redistribution of the beetles, then were left undisturbed until the next recording.

4.2.4 Treatment of the data

Numbers of beetles that had climbed per recording were expressed as percentages of each species total test beetles (40 in experiment 1, 20 in experiments 2 and 3). Percentages were transformed to arcsins (expressed in radians) of their square roots to be amenable to statistical analysis. Transformed values are hereafter referred to as climbing frequencies or scores.

4.2.5 Morphometric data

Legs are used in climbing and are thus the structures to examine for appropriate modifications. No peculiar structure, such as adhesive vestiture, was found but it was obvious at a glance that the species tested differed in body and in leg size.

Specimens that served in experiment 3 were killed upon termination of the tests, pinned and spread. The following measurements were taken on each specimen, under a dissecting microscope with an eyepiece micrometer at a magnification of 100 (one micrometer division equaled 0.00625 mm): (1) length of right posterior tibia; (2) length of right posterior tarsus (the sum of all articles measured individually); (3) standardized body length, i.e. the sum of head, pronotal and elytral length, measured individually (see Ball, 1972). These measurements were used in assessing possible morphological correlates of climbing frequency.

4.3 Results

4.3.1 Species tendencies to climb

Results of the three experiments are presented in Figures 18 - 20.

Experiment 1. Climbing frequencies differed in all four species tested during the day (Fig. 18a). *A. nigriceps* recorded the highest score, while *A. ferruginosum* and *A. thoreyi* were intermediate, and *A. cupreum*, the "control" species, had the lowest score.

During scotophase (Fig. 18b), all climbing scores increased, and *A. ferruginosum* frequency was the same as that of *A. nigriceps*. The relative magnitude of *A. thoreyi* score compared to that of *A. cupreum* was the same during the night as during the day.

Experiment 2. One species, *A. propinquum*, was added to the group tested. Day time climbing frequencies differed among species (Fig. 19a). *A. nigriceps* had the highest frequency, while *A. ferruginosum*, *A. thoreyi* and *A. propinquum* showed intermediate scores, the former two performing about equally but climbing more than the latter. Virtually no climbed individuals were recorded for *A. cupreum*.

During night time (Fig. 19b), *A. ferruginosum* and *A. propinquum* showed slightly higher climbing scores than during photophase, the former's frequency reaching that of *A. nigriceps*.

Figure 18. Climbing frequencies of *Agonum* species in experiment 1 (1978). Letters under bars stand for species names as follows:

N = *A. nigriceps*; F = *A. ferruginosum*;
T = *A. thoreyi*; C = *A. cupreum*.
(Means ± 1 SE).

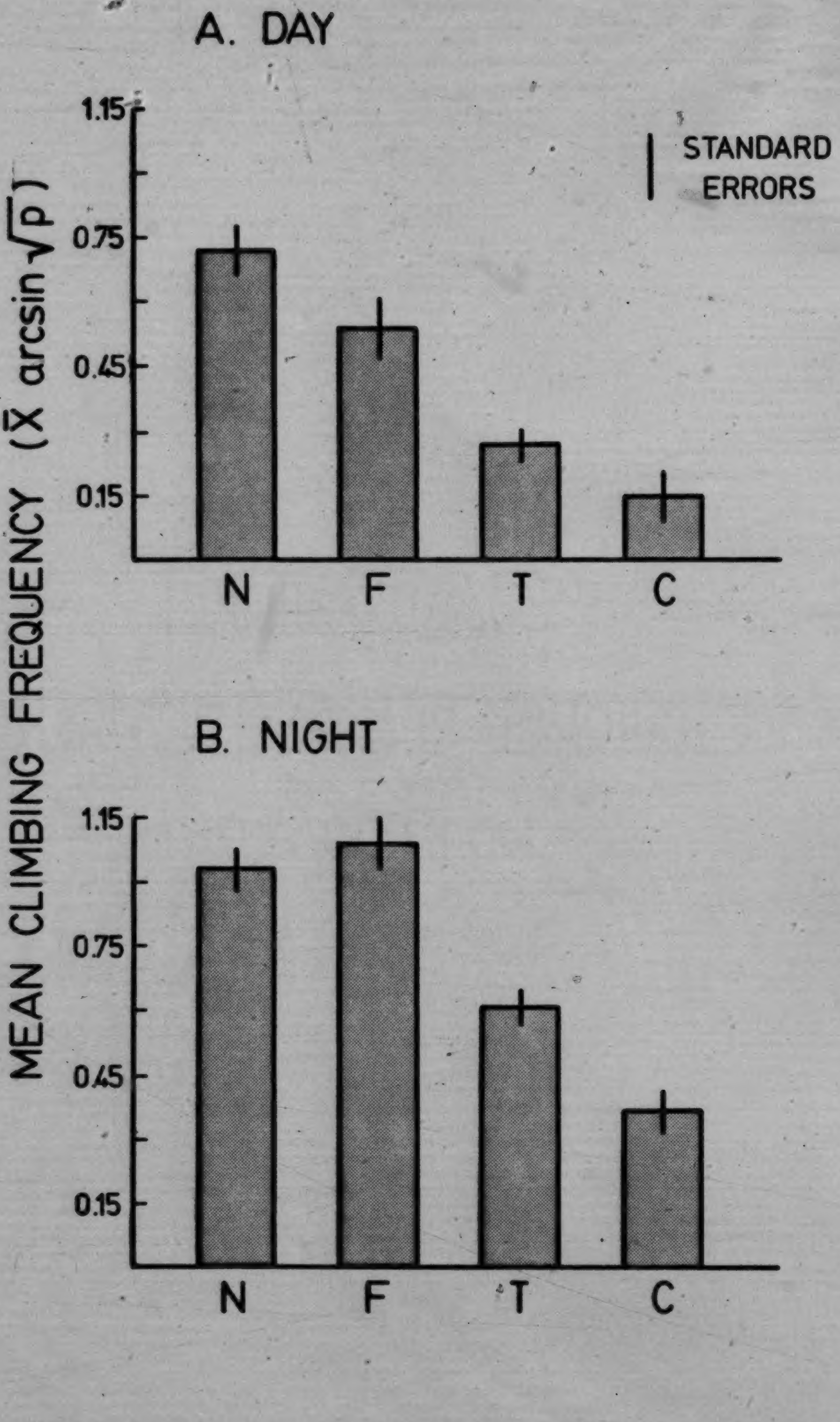

A. DAY
1.15
0.75
0.45
0.15
STANDARD ERRORS
N
F
T
C
MEAN CLIMBING FREQUENCY ($\bar{X}$ arcsin $\sqrt{p}$)
B. NIGHT
1.15
0.75
0.45
0.15
N
F
T
C

Figure 19. Climbing frequencies of *Agonum* species in experiment 2 (1979). Letters under bars stand for species names as follows:

N = *A. nigriceps*; F = *A. ferruginosum*;

T = *A. thoreyi*; P = *A. propinquum*;

C = *A. cupreum*.

(Means ± 1 SE).

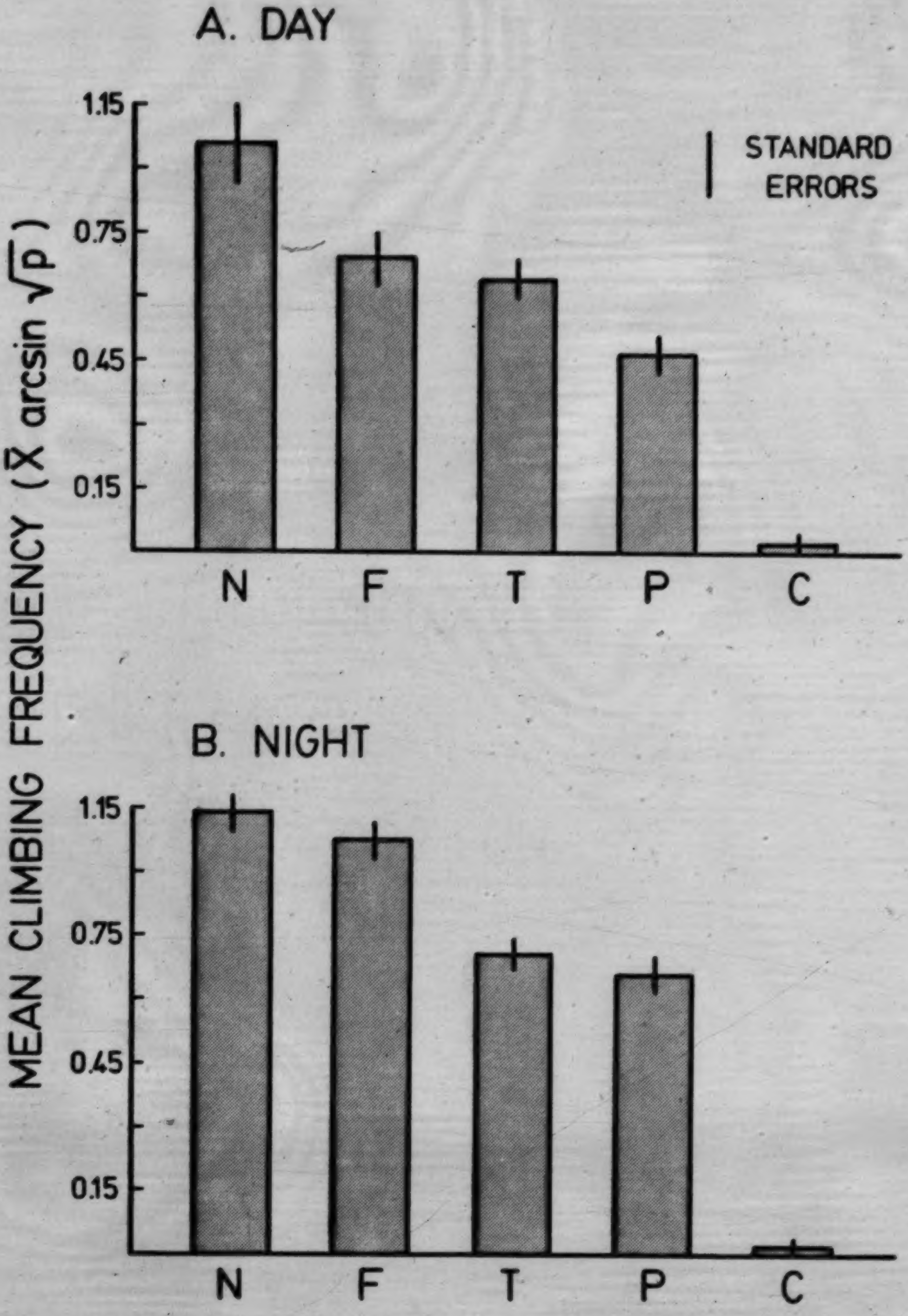
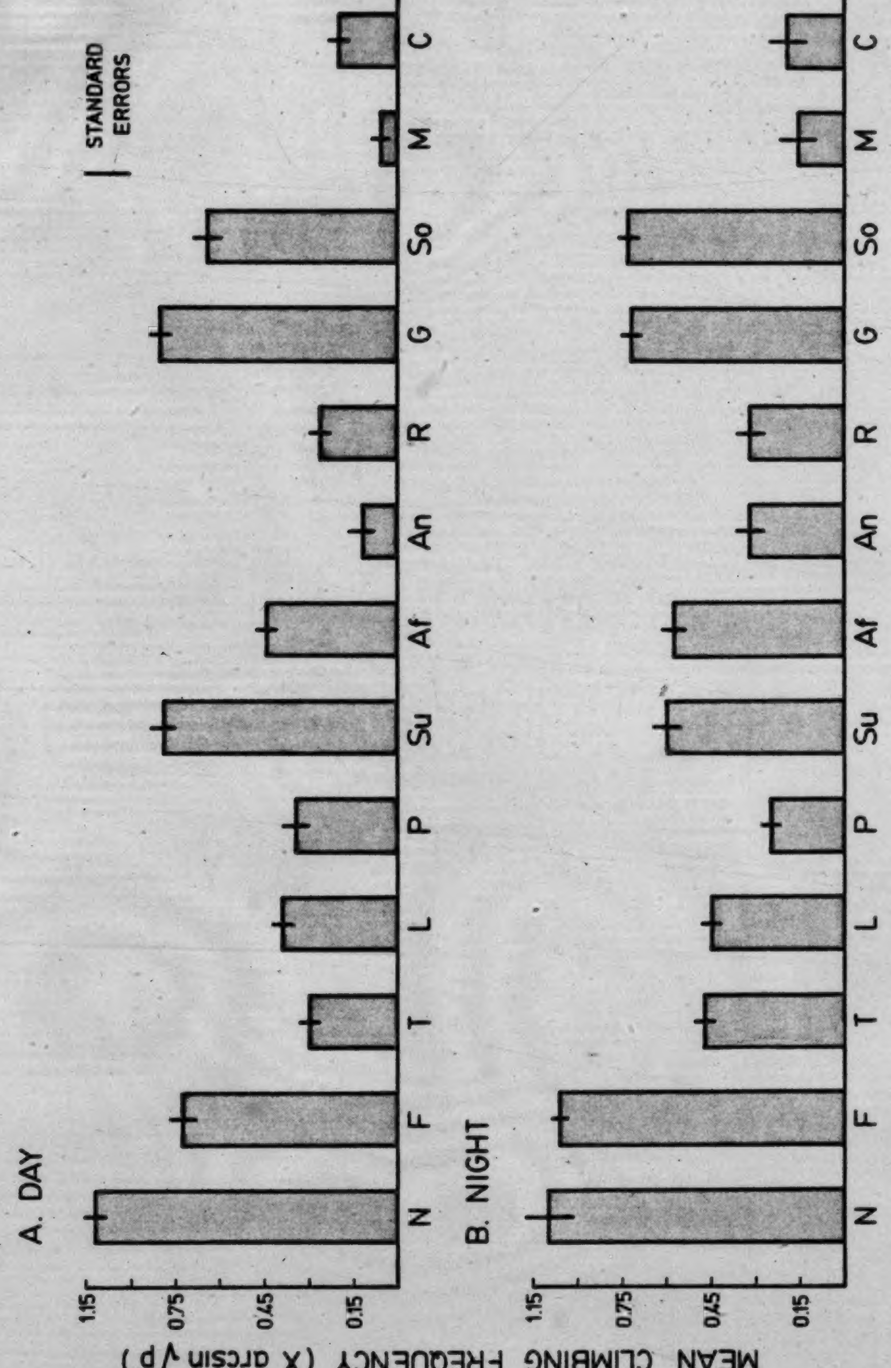

A. DAY
1.15
0.75
0.45
0.15
STANDARD ERRORS
N
F
T
P
C
MEAN CLIMBING FREQUENCY ($\bar{X}$ arcsin $\sqrt{p}$)
B. NIGHT
1.15
0.75
0.45
0.15
N
F
T
P
C

Figure 20. Climbing frequencies of *Agonum* species in experiment 3 (1980). Letters under bars stand for species names as follows:

N = *A. nigriceps*; F = *A. ferruginosum*;
T = *A. thoreyi*; L = *A. lutulentum*;
P = *A. propinquum*; Su = *A. superioris*;
Af = *A. affine*; An = *A. anchomenoides*;
R = *A. retractum*; G = *A. gratiosum*;
So = *A. sordens*; M = *A. mannerheimi*;
C = *A. cupreum*.
(Means ± 1 SE).


A. DAY
B. NIGHT
STANDARD ERRORS
MEAN CLIMBING FREQUENCY (X̄ arcsin √p)
1.15
0.75
0.45
0.15
N
F
T
L
P
Su
Af
An
R
G
So
M
C

Experiment 3. Both day and night climbing frequencies varied widely among the thirteen species tested (Fig. 20). *A. nigriceps* again scored highest, but was joined by *A. ferruginosum* at night. Intermediate scores were recorded for *A. gratiosum*, *A. superioris* and *A. sordens*, while the remaining species showed relatively low scores. Most species climbed slightly more during night time.

Results of the three experiments were evaluated with two-way analyses of variance, shown in Table 8. Differences among species were highly significant in all experiments. However in experiment 1, the effect of day-night conditions accounted for more of the observed variance than differences among species. For that experiment, it can thus be concluded that species differed in climbing frequency, but that day-night conditions had a more marked effect; however the effect of conditions did not alter the relative performance of the species.

Interactions between day-night conditions and species were significant in both experiment 2 and 3, but differences among species absorbed a much greater proportion of the variance than both conditions and interactions. The effect of conditions was not significant. Therefore in these experiments, it can also be concluded that species differed in climbing frequency, but that relative extent of performance for most species varied slightly between day and night.

TABLE 8

Two-way analyses of variance
for the percentage of beetles that climbed sedge straws

A. EXPERIMENT 1 (1978)

SOURCE	df	S.S.	M.S.	F	p
Species	3	4.17	1.39	35.74	<.001
Day-night	1	2.45	2.45	62.85	<.001
Interactions	3	0.23	0.08	1.98	.122
Remainder	88	3.43	0.04		

B. EXPERIMENT 2 (1979)

SOURCE	df	S.S.	M.S.	F	p
Species	4	25.33	6.33	41.34*	<.005
Day-night	1	1.08	1.08	7.04*	>.050
Interactions	4	0.61	0.15	2.43	.048
Remainder	253	15.90	0.06		

C. EXPERIMENT 3 (1980)

SOURCE	df	S.S.	M.S.	F	p
Species	12	44.72	3.73	20.72*	<.001
Day-night	1	0.33	0.33	1.83*	>.100
Interactions	12	2.15	0.18	5.89	<.001
Remainder	559	16.98	0.03		

* tested over interactions M.S.

The salient points to retain about the results are the following: (1) *A. nigriceps* consistently showed the highest climbing scores in all experiments, both during day and night time; (2) in all experiments, *A. ferruginosum* climbed more during the night than during the day, and at night its climbing score equaled that of *A. nigriceps*; (3) species known to occur in the unflooded zone of the marsh generally showed intermediate climbing frequencies; (4) climbing scores of the "control" species were among the lowest. Despite discrepancies among results of the experiments, probably owing in part to differences in conditions (see Material and Methods), and the limited scale of these tests, the artificial settings were sufficient to evoke responses among the species that roughly supported the hypothesis.

4.3.2 Leg size and climbing

Means of standardized body length (SBL), posterior tibia and posterior tarsus lengths, along with the species overall climbing scores (from day and night data pooled) are provided in Table 9 for all species tested. Relationships between morphometric data and climbing scores were examined with correlation analysis. Pearson's correlation coefficients (Table 10a) revealed that all three morphological features were significantly correlated with climbing scores. All coefficients were negative indicating that climbing frequency increased with smaller body size and shorter posterior tibiae and posterior tarsi. However very

TABLE 9

Mean values of body and leg measurements
and overall climbing scores
for the species of *Agonum* tested in climbing experiment 3

SPECIES	OVERALL CLIMBING SCORE	SBL (mm)	LENGTH OF POSTERIOR TIBIA (mm)	LENGTH OF POSTERIOR TARSUS (mm)
A. nigriceps	1.115	5.22	1.49	1.51
A. ferruginosum	0.840	5.99	1.73	1.43
A. gratiosum	0.757	6.42	2.14	1.84
A. superioris	0.696	6.44	1.93	1.57
A. sordens	0.682	5.22	1.57	1.21
A. affine	0.501	8.19	2.34	1.86
A. lutulentum	0.418	5.87	1.73	1.50
A. thoreyi	0.378	6.76	2.05	1.78
A. propinquum	0.297	6.55	1.91	1.49
A. retractum	0.289	5.92	1.84	1.38
A. anchomenoides	0.210	6.03	1.87	1.63
A. cupreum	0.191	8.10	2.40	2.09
A. mannerheimi	0.106	9.50	3.28	2.83

TABLE 10

Pearson's and partial correlation coefficients
for morphometric data and climbing scores from experiment 3

A. PEARSON'S CORRELATIONS

	POSTERIOR TIBIA	POSTERIOR TARSUS	CLIMBING SCORE
SBL	.961 (<.001)	.931 (<.001)	-.586 (.035)
POST. TIBIA		.962 (<.001)	-.591 (.034)
POST. TARSUS			-.483 (.094)

B. FIRST-ORDER PARTIALS

VARIABLE CORRELATED WITH SCORE	VARIABLE HELD CONSTANT		
	SBL	POST. TIBIA	POST. TARSUS
SBL	--	-.083 (.798)	-.406 (.191)
POST. TIBIA	-.122 (.706)	--	-.524 (.080)
POST. TARSUS	.156 (.628)	.383 (.219)	-

C. SECOND-ORDER PARTIALS

VARIABLE CORRELATED WITH SCORE	VARIABLES HELD CONSTANT		
	SBL+ POST. TIBIA	SBL+ POST. TARSUS	POST. TIBIA+ POST. TARSUS
SBL	--	--	-.028 (.936)
POST. TIBIA	--	-.365 (.270)	--
POST. TARSUS	.376 (.255)	--	--

Numbers in parentheses are significance levels.

marked correlations among the three sets of morphometric data suggest allometric effect of body size on leg length.

In order to assess the independent contribution of each morphological parameter to the relationship with climbing scores, first- and second-order partial correlation coefficients were computed (Table 10b and 10c). With the effect of posterior tibia controlled (Table 10b), correlation of SBL with climbing score was reduced. There was also a reduction in that relation with posterior tarsus length held constant. Correlations of both leg parameters were markedly reduced with effect of body size controlled, but it is interesting to note that the coefficient changed sign. With both leg parameters controlled simultaneously, the second-order partial for SBL (Table 10c) became essentially 0, indicating that the relationship between body size and climbing frequency was spurious. In contrast, second-order partials for both tibia and tarsus length were higher that their first-order counterparts. Even though second-order partials for leg parameters are not statistically significant, they suggest an interesting trend: higher climbing scores would tend to be associated with longer posterior tarsi but with shorter posterior tibiae. Morphological features of the legs accounted for little of the observed variation in mean climbing score (13% and 14% for posterior tibiae and posterior tarsi respectively). Nevertheless the data of Table 10 reveal that adults of *A. nigriceps*, the species with the highest climbing score, are the only ones to possess posterior tibiae that are shorter than the posterior tarsi.

4.4 Discussion

4.4.1 Habitat structure and climbing

The highest climbing frequency of *A. nigriceps* adults is consistent with its more frequent occurrence than adults of other species in structurally simple, less dense patches of vegetation of the flooded marsh. Such patches imply for foraging beetles the use of narrow vertical stems. The tendency of *A. nigriceps* adults to rest on similar structures in the laboratory may explain why their distribution in the marsh appeared insensitive to microhabitat features (see Chapter 2).

On the other hand, *A. ferruginosum* and *A. thoreyi* adults had lower climbing scores and this is correlated with their marked association with patches of dense dead vegetation, where the compact, intricate structure probably makes it easy for them to forage without much climbing. The association of *A. thoreyi* adults with emergent substrate and with unflooded macrohabitats may further explain their lower climbing frequency than that of *A. ferruginosum* adults. Knowledge of microhabitats of *A. lutulentum* is scanty but would suggest an explanation similar to that given for *A. ferruginosum* or *A. thoreyi*.

It was consistently observed that *A. ferruginosum* adults climbed as much as those of *A. nigriceps* during the night but had a lower climbing frequency during the day. This behavioral pattern may be linked to nocturnal activity of the former group (Chapter 3). In connection with greater occurrence than *A. nigriceps* in densely vegetated patches, this may reflect a different preference of *A. ferruginosum* adults for resting sites during day-light hours.

Species-specific behaviors observed in the experiments therefore generally support the hypothesis set forth in Chapter 2 that the vegetation structure may affect the species distributions within the flooded zone. Given the limited scale of the experiments performed and lack of knowledge of mechanisms underlying habitat associations, explanations for some of the differences are not possible; such differences may indeed be part of the normal behavioral flexibility of these carabids. Experiments such as these obviously have limitations and biases. Marked thigmotactic reflexes and light avoidance reactions (all species tested except perhaps *A. cupreum* are in all probability nocturnal) make them difficult subjects for manipulation. Further tests of climbing behavior might attempt to provide some form of shelter in addition to the substrate offered. However the addition of factors might greatly complicate analysis of the data and interpretation of the results.

4.4.2 Leg size and climbing

Lack of significant correlation between climbing and leg structure does not negate the possibility of a real relationship. Beside possible biases in responses caused by artificial conditions, a linear model such as that of correlation analysis may not best describe the pattern. It is likely that much of the contribution to the correlation is accounted for by *A. nigriceps*.

Short tibiae and long tarsi obviously present an advantage for increasing climbing ability on narrow structures such as plant stems. *A. nigriceps* is the species whose adults possess this trait developed to the highest degree, with tarsi that are even longer than tibiae. Klopfer (1969: 55) has noted that very minor morphological differences can lead to substantial ones in relative success of exploitation of particular habitats. In carabids, profound morphological adaptations are known that are related to habitat exploitation (Thiele, 1977: 3ff), but minor adaptations have also been recorded (Andersen, 1978). In tropical arboreal species, tarsal modifications apparently enable adults of the species that possess these to run on tree foliage (Erwin, 1978). In water-striders, Spence (1979b) reported that leg length was related to foraging efficiency in emergent vegetation. Present data suggest that *A. nigriceps* adults also possess morphological adaptations in the relative size of their leg segments that allow efficient foraging in their habitat. Evolution of niche relationships, and especially habitat differentiation among *Agonum* members of the marsh guild might have been guided to some extent by differences in capability or in pre-adaptations to use structure of vegetation.

4.4.3 Climbing and crypsis in *A. nigriceps*

Lindroth (1966: 584) noted that the yellow ground color and striped pattern of *A. nigriceps* adults is unique among *Agonum*, which are generally dark colored carabids[3]. This coloration is puzzling as regards its origin. G.E. Ball (pers. comm.) is not aware of any species that may be phylogenetically related to *A. nigriceps* on the basis of color. The flat body, fragile appearance and coloration remind one of European *Demetrias* or *Dromius* adults (Lindroth, 1966: 583) which coincidentally are also climbers (arboreal). But relationships with them are precluded because they belong to a different tribe (Lebiini) and the superficial resemblance is probably the result of convergence.

A likely explanation for the coloration of *A. nigriceps* adults is that it constitutes a cryptic pattern matching the background of its principal habitat —namely sedge. Figure 21 shows a sketch of an individual of *A. nigriceps* in a typical resting posture on a sedge leaf. During day time, beetles are observed on sedge blades positioned in that characteristic manner, many in very exposed sites (e.g. edge of a tussock). The antennae are held parallel to one another in line with the longitudinal axis of the body, pointing in

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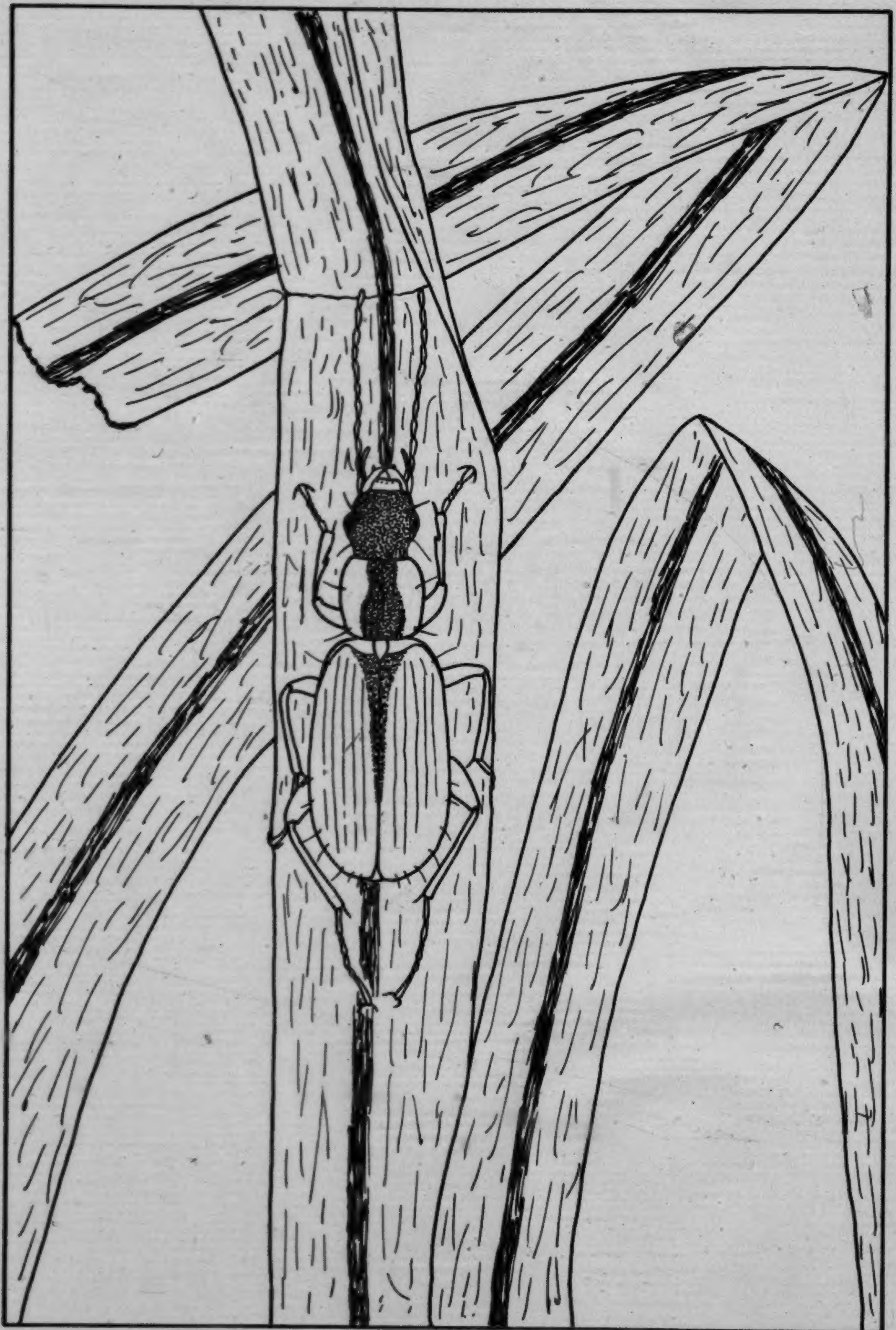
[3] *A. nigriceps* adults are sexually dimorphic relative to color: males have shiny black abdominal sterna, while females have entirely pale yellow sterna. This is independent of wing condition. This character apparently eluded Lindroth (1966) who described the species (p. 584) as "pale yellow, abdomen darker, head black...".

Figure 21. Typical resting posture of *A. nigriceps* on a sedge leaf.



a most unusual forward direction. I have not observed any other carabid adults holding their antennae in that way. In *A. nigriceps*, this position of the antennae almost seems to be a reflex once at rest. In addition, legs are held along the body. Beetles thus positioned seem to flatten themselves on leaves or stems. Blending with the vegetation is amazing in the field, and beetles may easily elude an untrained eye. Such postures were also observed in the climbing experiments.

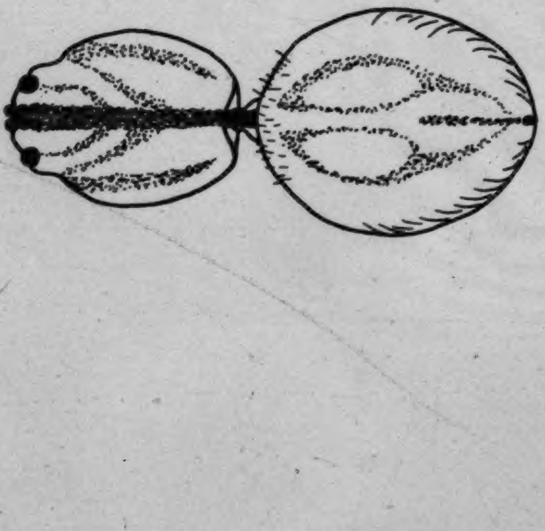
Another line of support for the crypsis hypothesis comes from arthropods found with *A. nigriceps* among the dead sedge growth or at the base of growing shoots (the base of these shoots is frequently yellowish brown with blackish veins). In particular some spiders display a very similar color pattern (Figure 22). This is most remarkable for *Pachygnatha tristriata* specimens, a tetragnathid species, whose cephalothoraces show a pattern much resembling that of the pronotum and elytra of *A. nigriceps* adults. Indeed during field surveys I frequently picked these spiders among the submerged plants when they had their abdomen hidden, mistaking them for *A. nigriceps*. Several other arthropods and invertebrates co-occurring with *A. nigriceps* have a yellow ground color marked with dark spots or lines (among them were chrysomelid and coccinellid beetles, leafhoppers and snails). All seem to inhabit the lower stratum of the flooded sedge and cattail vegetation which is characteristically yellowish brown.

Figure 22. Body outlines of *A. nigriceps* and of spiders found in the marsh vegetation.

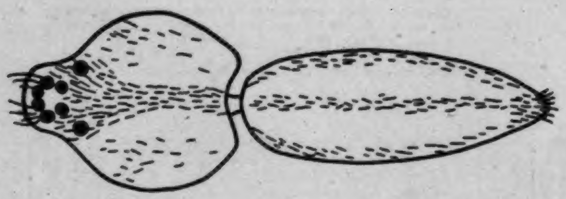
A. *Pachygnatha tristriata* (11.5 X)

B. *Tibellus oblongus* (12.5 X)

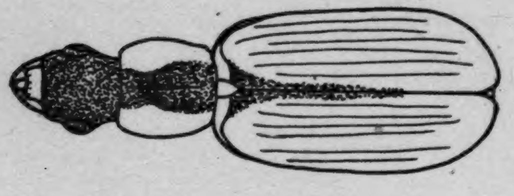
C. *A. nigriceps* (11.5 X).



A



B



C

A cryptic coloration may be advantageous for protection against visually hunting predators. Examples of mimicry possibly involving predator avoidance have been described in carabids of the genus *Lebia* (Lindroth, 1971). Blending with the habitat background is well known among insects as a means of reducing predator efficiency, and may have evolved in *A. nigriceps* to reduce conspicuousness of its adults on the relatively open vegetation of their habitat.

5. COMMUNITY ANALYSIS AND GUILD STRUCTURE

5.1 Introduction

Following the formal moulding of the niche concept into the hypervolume model (Hutchinson, 1957, 1965: 32ff), theoretical and empirical works have attempted to provide the model with feasible approximations to field data. Several metrics have been proposed to express observed patterns of resource partitioning in comparable synthetic quantitative measures (Horn, 1966; MacArthur and Levins, 1967; MacArthur, 1968; Levins, 1968; Colwell and Futuyma, 1971; May and MacArthur, 1972; Roughgarden, 1972; Pianka, 1973).

Most niche metrics have been devised with implicit assumptions of operating competition (MacArthur, 1968; Vandermeer, 1972; Cody, 1974), which is generally assumed to be the pervasive force leading to and maintaining segregation of species along niche axes. Some such measures of distribution of co-occurring species over shared resource spectra have even been equated with estimates of competition coefficients, notably the a's of the Lotka-Volterra equations (Vandermeer, 1972; Hutchinson, 1978: 165ff). Criticisms have been levelled at the latter course of action as being inappropriate (Sale, 1974; Pianka, 1975; Whittaker and Levin, 1975: 175; Lawlor, 1980), because differential resource use is no proof of continued competition (Wiens, 1977).

Although niche measures, such as the frequently used breadth and overlap, obviously have shortcomings and must be used with caution in comparisons (Whittaker and Levin, 1975: 172; Pianka, 1978: 245), they are useful because they afford a means of organizing field data and may help in elaboration or testing of generalizations for niche theory (Colwell and Futuyma, 1971).

In the preceding chapters, I have shown that *Agonum* species distributions within marshes were sensitive to habitat heterogeneity (Chapter 2), and that there were also differences in timing among species (Chapter 3). The analysis of this chapter was undertaken to describe the patterns of partitioning of these carabids in a more general way, using some of the techniques developed for niche analysis. I also assess the potential occurrence of interspecific interactions and the possible importance of size differences among the dominant members of the guild.

5.2 Methods

5.2.1 Niche breadth

Niche breadth of a species represents its spreading along a resource axis or set of resource states. It was determined by Levins (1968: 43):

$$B = (n \sum Pi^2)^{-1}$$

where Pi is the proportion of the species in the ith resource unit (or state), and n represents the number of resource units studied. The breadth B can take values from 1/n to 1.0. A value of 1.0 indicates equal distribution over all resource states, while a value of 1/n indicates concentration in a single resource state. Breadth values of the dominant species of *Agonum* were computed with respect to macrohabitats, microhabitats and breeding time. For the latter, proportions of egg-carrying females from the seasonal total were used.

5.2.2 Niche overlap

The niche overlap index is a measure of the degree to which two species share a resource set, and was determined by Pianka (1973, 1974):

$$Ox = Oy = (\sum Xi.Yi) / (\sum Xi^2 \sum Yi^2)^{0.5}$$

where Xi and Yi are the relative abundances of species x and y with respect to the ith resource unit. The main advantage of using this index of overlap instead of other measures (e.g. Levins, 1968: 51) is its symmetry for the species concerned. The superiority of this formula over non-symmetrical ones was demonstrated by May (1975) and discussed by Slobodchikoff and Schulz (1980).

Overlap values were computed for all species pairs of the marsh community with respect to macrohabitats. Overlaps in macrohabitats, microhabitats and breeding time were calculated for the numerically most abundant *Agonum*. For microhabitats, two overall overlap values were computed: one by taking the product of overlap values from individual microhabitats, and one by calculating their arithmetic mean. The two resulting values provided a lower and an upper bound of overlap estimation over combined resource sets (May, 1975; Pianka, 1975).

5.2.3 Dendrograms

Macrohabitat relationships of the marsh community were studied by means of dendrograms based on degree of overlap among species. The method of computation of overlap values is described in the preceding section. Dendrograms were derived from overlap matrices according to the technique described by Cody (1974: 92ff), which is in essence a simplified clustering method. Briefly, the technique combines the species pair having the highest overlap value into a unit whose new overlap with each other member of the community is the arithmetic mean of the respective overlaps of the two component species prior to their combination. This combination procedure is repeated until all species and units are clustered.

Species with only one sampled individual, or obvious stragglers (e.g. two long-winged *A. decentis* were found in the cattails) were excluded from the analysis. Species with very low numbers were included if their occurrence in the marsh matched their known general habitat (based on Lindroth, 1955b, 1961, 1966).

5.2.4 Spatial association analysis

Empirical evidence for interspecific competition is indicated if distribution and/or abundance of two or more species are mutually exclusive, or at least negatively correlated.

To measure spatial association among species, numbers of captures of each species in particular samples were used to calculate Kendall's coefficients of rank correlation. Only samples with ten or more beetles (from all species pooled) were selected for analysis. Separate correlations were then evaluated for sets of samples from different macrohabitats. Each species was tested against all others combined.

5.2.5 Size relationships

Groups of beetles belonging to the four dominant *Agonum* species collected at the main study sites were measured. Measurements were taken as described in Chapter 4 (section 4.2.5). Standardized body length, used as an index of body size, and labrum width, taken as an index of mouth size, were recorded and compared among species.

5.3 Results

5.3.1 Macrohabitat relationships of the community

Dendrograms showing relationships of macrohabitat overlap among members of the marsh carabid community are presented in Figures 23 and 24 for George Lake and Barrhead respectively.

The George Lake community (Fig. 23) can be divided into two major groups or guilds (here *sensu* Root, 1967): one to the left of the dendrogram, including *A. mannerheimi* to *A. sordens*, a cluster of species whose adults principally inhabit the unflooded portion of the marsh, and one comprising *A. anchomenoides* to *A. lutulentum*, whose adults live mainly in the flooded zone. The guild from the unflooded zone can be further divided into two sub-guilds: the one of *A. mannerheimi* to *A. gratiosum* roughly occupies the wet forest margin while the one formed by *A. superioris* to *A. sordens* is mainly found in the unflooded sedge. Overlaps within these two sub-guilds reach extremely high values indicating tight species packing. In contrast, the flooded marsh guild is much more loosely organized, as species pairs show on average lower overlap values.

One species, *Blethisa multipunctata*, appears to be sandwiched between the two major guilds, as distribution of its adults was split between the flooded and unflooded marsh zones. Very few specimens of this species were captured by the quadrat method, but data from pitfall catches and hand

Figure 23. Dendrogram showing grouping by overlap values for macrohabitat of the marsh carabid community at the George Lake study site.

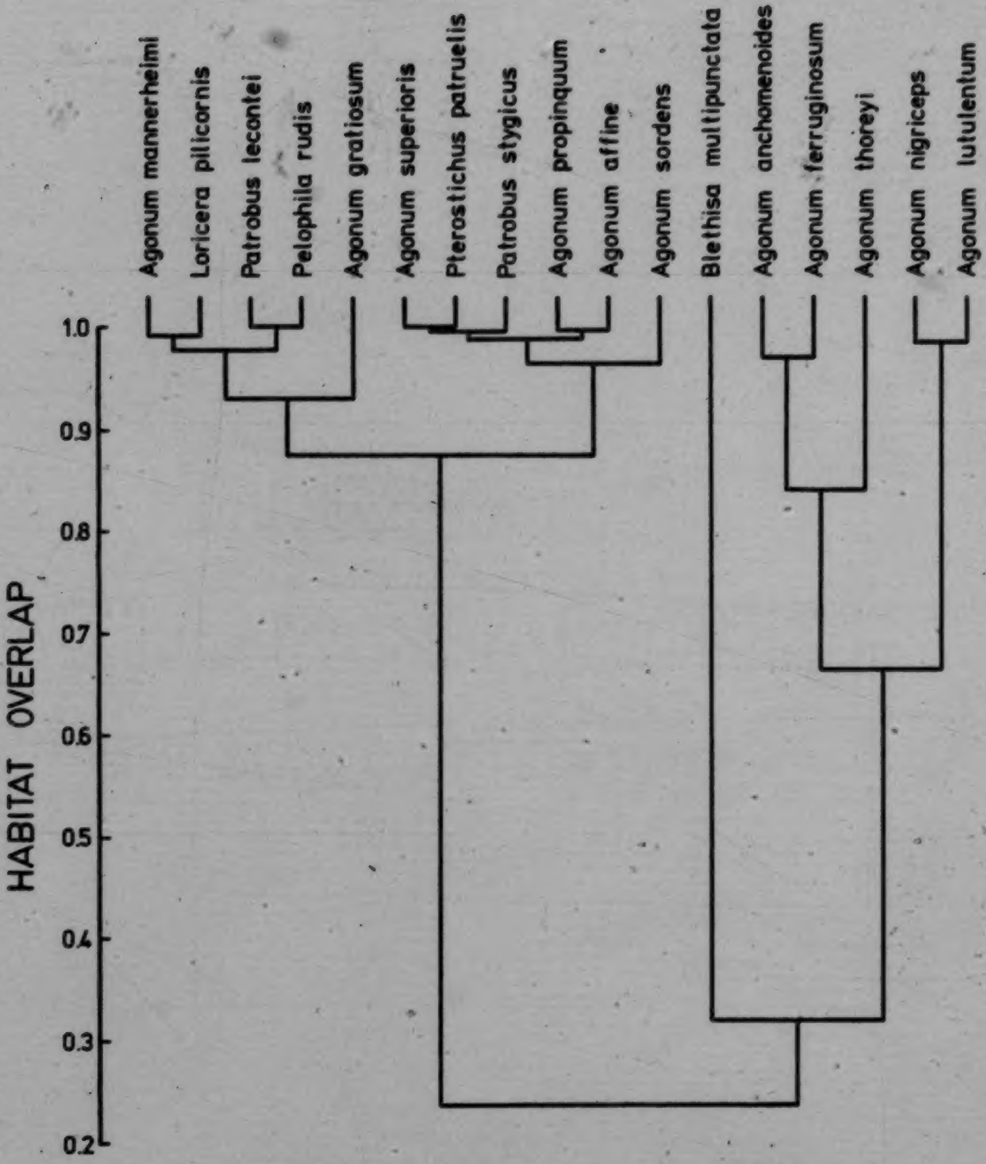
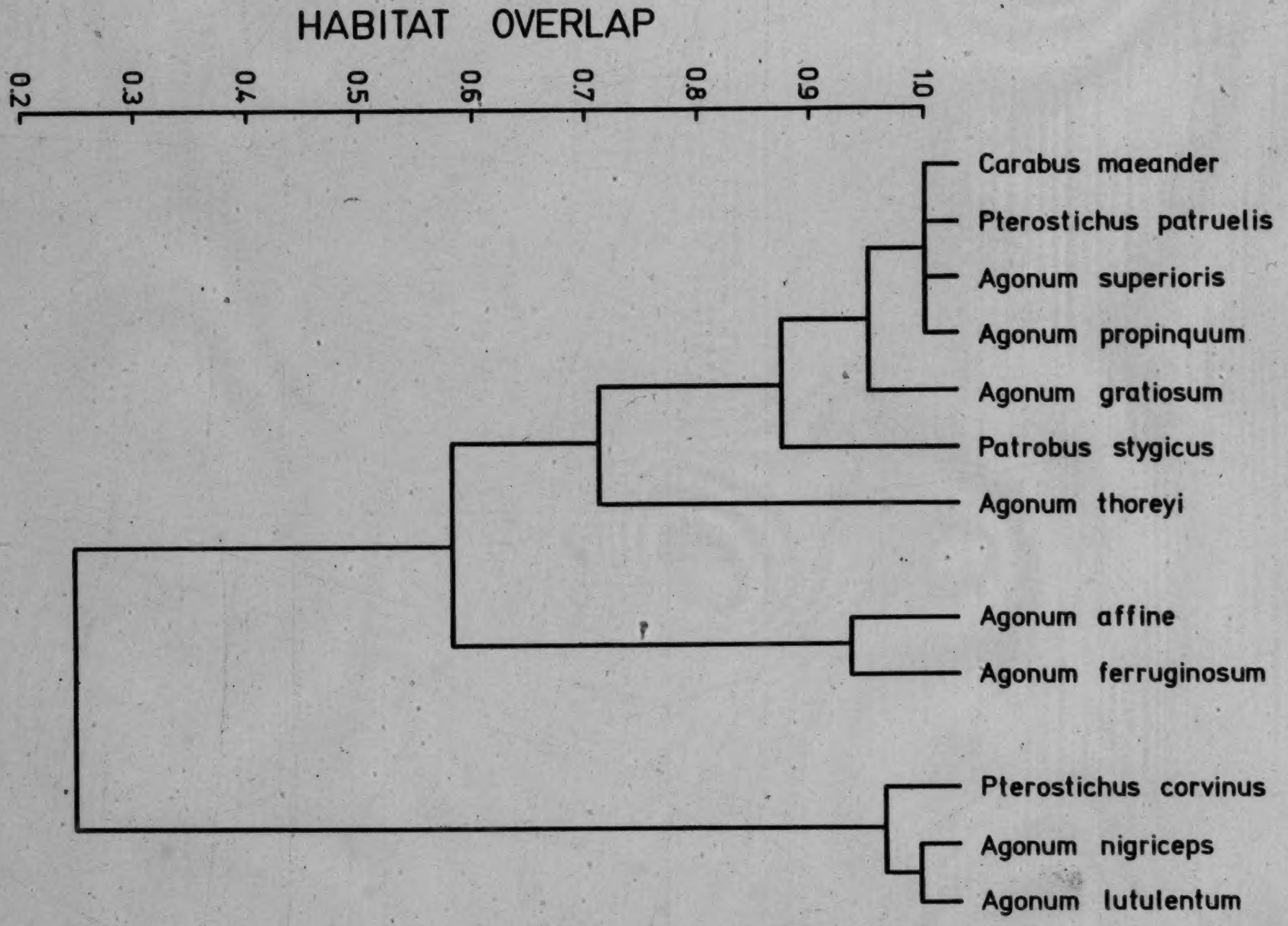

HABITAT OVERLAP
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
Agonum mannerheimi
Loricera pilicornis
Patrobus lecontei
Pelophila rudis
Agonum gratiosum
Agonum superioris
Pterostichus patruelis
Patrobus stygicus
Agonum propinquum
Agonum affine
Agonum sordens
Blethisa multipunctata
Agonum anchomenoides
Agonum ferruginosum
Agonum thoreyi
Agonum nigriceps
Agonum lutulentum

Figure 24. Dendrogram showing grouping by overlap values for macrohabitat of the marsh carabid community at the Barrhead study site.


HABITAT OVERLAP
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Carabus maeander
Pterostichus patruelis
Agonum superioris
Agonum propinquum
Agonum gratiosum
Patrobus stygicus
Agonum thoreyi
Agonum affine
Agonum ferruginosum
Pterostichus corvinus
Agonum nigriceps
Agonum lutulentum

collecting would suggest that *B. multipunctata* belongs to the guild from the unflooded zone.

The Barrhead community (Fig. 24), poorer in species than the George Lake one (see Chapter 2 for discussion) displays generally lower overlap values. Three groups more or less clearly emerge: one loosely encompassing *Carabus maeander* to *A. thoreyi*, one formed by the pair *A. affine-A. ferruginosum*, and one composed of *Pterostichus corvinus* to *A. lutulentum*. These correspond approximately to an unflooded sedge group, a group distributed over both unflooded and flooded sedge, and a group mainly concentrated in sedge tussocks. The looser relationships (lower overlap) among some of the members of the first group emphasizes the relative nature of the grouping and shows that some component members were not entirely restricted to the unflooded portion of the marsh (especially *A. thoreyi*). However high overlap is present among some of the members of each guild.

In order to assess a relationship between macrohabitat overlap and species abundance, species densities were estimated by dividing the total catch for each species in a given macrohabitat by the total number of samples from that habitat. These densities were then averaged for each macrohabitat.

Table 11 shows the average density of carabids in macrohabitats at both main study sites. Values are generally much lower in unflooded than in flooded zone, and small

TABLE 11

Average species densities in macrohabitat categories at the two main study sites

MACROHABITAT	N OF SPECIES	MEAN DENSITY 0.25 m^{-2}	s^2
GEORGE LAKE			
wet forest margin	15	0.24	0.03
unflooded sedge meadow	15	0.29	0.13
flooded sedge meadow	9	0.77	1.28
sedge tussocks	7	1.33	3.31
floating cattails	10	1.42	9.00
BARRHEAD			
unflooded sedge meadow	13	0.35	0.56
flooded sedge meadow	6	0.97	1.59
sedge tussocks	6	1.50	3.10
floating cattails	6	0.50	0.24

variances are associated with low densities (low densities in the Barrhead cattails were already discussed in Chapter 2). These results indicate that as overall abundance increased, a few species became markedly dominant (numerically), and thus diversity decreased. The very small variance observed at the forest margin (George Lake) indicates markedly uniform abundances among species found in that habitat zone, hence very high diversity. These results examined in conjunction with the dendrograms show that on average, high overlap values (guilds from the unflooded zone) tend to be associated with low species abundances.

5.3.2 Niche breadth

Niche breadths of the dominant species of *Agonum* for three resource sets are presented in Table 12. Breadth values given for microhabitats represent means of four sets of microhabitats, namely patches of dead sedge, sedge tussocks, patches of dead cattail and cattail substrate, each with two resource states.

On the macrohabitat dimension, *A. thoreyi*, whose adults are habitat generalists, had the largest breadth which took virtually identical values at both marshes. At George Lake, *A. nigriceps* had an intermediate niche breadth; *A. ferruginosum* had the narrowest breadth as a result of its strong peak in the cattails (Chapter 2). At Barrhead, *A. lutulentum* had the narrowest niche, while the relative ranking of *A. ferruginosum* and *A. nigriceps* was the reverse

TABLE 12

Values for niche breadth and abundance rank of the dominant species of marsh *Agonum* with respect to three resource sets

RESOURCE SETS		SPECIES OF *Agonum*		
		nigriceps	*ferruginosum*	*thoreyi*
macrohabitats	GL[1]	0.540	0.482	0.807
	B[2]	0.474	0.597	0.810
microhabitats		0.941	0.729	0.720
breeding time		0.887	0.757	0.702
abundance rank	GL	2	1	3
	B	2	3	1

[1] Abbreviations: GL=George Lake; B=Barrhead.

[2] Habitat breadth of *A. lutulentum* at Barrhead = 0.437, abundance rank = 4.

of that at George Lake.

With respect to microhabitats, *A. nigriceps* had the broadest distribution. *A. ferruginosum* and *A. thoreyi* had narrower, relatively similar breadths, mainly resulting from their concentration in densely vegetated habitat patches.

On the time dimension, *A. nigriceps* again showed the broadest niche. *A. ferruginosum* was intermediate, and *A. thoreyi*, breeding later, was the most narrowly spread.

Thus *A. nigriceps* can be qualified as a generalist with respect to microhabitats and time of breeding, but tends to be restricted in the macrohabitat occupied. *A. thoreyi* is a macrohabitat generalist but is the most restricted in both microhabitats and breeding time. *A. ferruginosum* occupies an intermediate position over both microhabitats and time, but displays a somewhat variable position with respect to macrohabitats.

Discrepancies observed between the two marshes in macrohabitat breadth for *A. nigriceps* and, more pronounced, for *A. ferruginosum* suggest that this dimension of the niche is the most flexible one among members of the flooded marsh guild. There was no consistent relationship between species abundance and breadth within the guild.

5.3.3 Niche overlap

Overlap values for pairs of the three dominant *Agonum* species are provided in Table 13. Values relating *A. lutulentum* to other members of the guild are not given

TABLE 13

Overlap values for three resource sets
among the dominant species of marsh *Agonum*
at George Lake site

SPECIES PAIRS	RESOURCE SETS				OVERALL	
	MACRO-HABITATS	MICROHABITATS		BREEDING TIME	LOWER LIMIT	UPPER LIMIT
		LOWER LIMIT	UPPER LIMIT			
A. nigriceps *A. ferruginosum*	0.644	0.740	0.906	0.943	0.500	0.803
A. nigriceps *A. thoreyi*	0.764	0.656	0.869	0.882	0.514	0.803
A. ferruginosum *A. thoreyi*	0.900	0.876	0.959	0.775	0.640	0.864

because of incomplete data.

The data show that within all three pairs, high overlap along one or two niche dimensions is associated with lower values along the third dimension. This pattern is more pronounced for the pairs *A. nigriceps-A. ferruginosum* and *A. ferruginosum-A. thoreyi*.

It also appears that the pairs *A. nigriceps-A. ferruginosum* and *A. nigriceps-A. thoreyi* are mainly segregated over the spatial (macrohabitat) dimension, while the pair *A. ferruginosum-A. thoreyi* is more markedly differentiated along the time dimension. These results suggest that different factors may be operating on different species to cause the observed segregation patterns.

Overall overlap values (medians of microhabitat overlaps were used in computing these) show that similarity in spatial and temporal resource use is greatest between *A. ferruginosum* and *A. thoreyi*, while *A. nigriceps* overlaps equally and to a lesser extent with the two former species.

5.3.4 Spatial association

Kendall's rank correlation coefficients (Tau's) for various combinations of the major species present simultaneously in samples are given in Table 14 for three macrohabitats at the two main study sites. A few representatives of these abundance relationships are depicted graphically in Figure 25. The rationale for testing single species against the remaining ones lumped together

TABLE 14

Association indices (Kendall's Tau) between co-abundances of marsh *Agonum* species in samples from various macrohabitat classes

SPECIES	CO-OCCURRING SPECIES IN SAMPLE	SITE AND MACRO-HABITAT[1]	TAU	p	N[2]
A. nigriceps	*A. ferruginosum* *A. thoreyi*	GL-FSM	-.512	.101	8
		GL-ST	-.302	.132	15
		GL-FC	-.376	.006	32
A. nigriceps	*A. ferruginosum* *A. thoreyi* *A. lutulentum*	B-ST	-.062	.730	18
A. ferruginosum	*A. nigriceps* *A. thoreyi*	GL-FSM	-.415	.164	8
		GL-ST	0.0	.999	15
		GL-FC	-.230	.083	32
A. ferruginosum	*A. nigriceps* *A. thoreyi* *A. lutulentum*	B-ST	.187	.372	18
A. thoreyi	*A. nigriceps* *A. ferruginosum*	GL-FSM	-.370	.209	8
		GL-ST	.109	.603	15
		GL-FC	-.139	.297	32
A. thoreyi	*A. nigriceps* *A. ferruginosum* *A. lutulentum*	B-ST	-.289	.107	18
A. lutulentum	*A. nigriceps* *A. ferruginosum* *A. thoreyi*	B-ST	-.207	.261	18

[1] Site and macrohabitat designations: GL=George Lake; B=Barrhead; FSM=flooded sedge meadow; ST=sedge tussocks; FC=floating cattails.

[2] Number of samples with catch ≥10.

Figure 25. Plots of pairwise numbers of individuals of the main species of *Agonum* found in the same samples. Vertical axes are abundances for single species indicated above each graph. Horizontal axes are abundances of the other species in the samples; these are the complements of either of the following series:

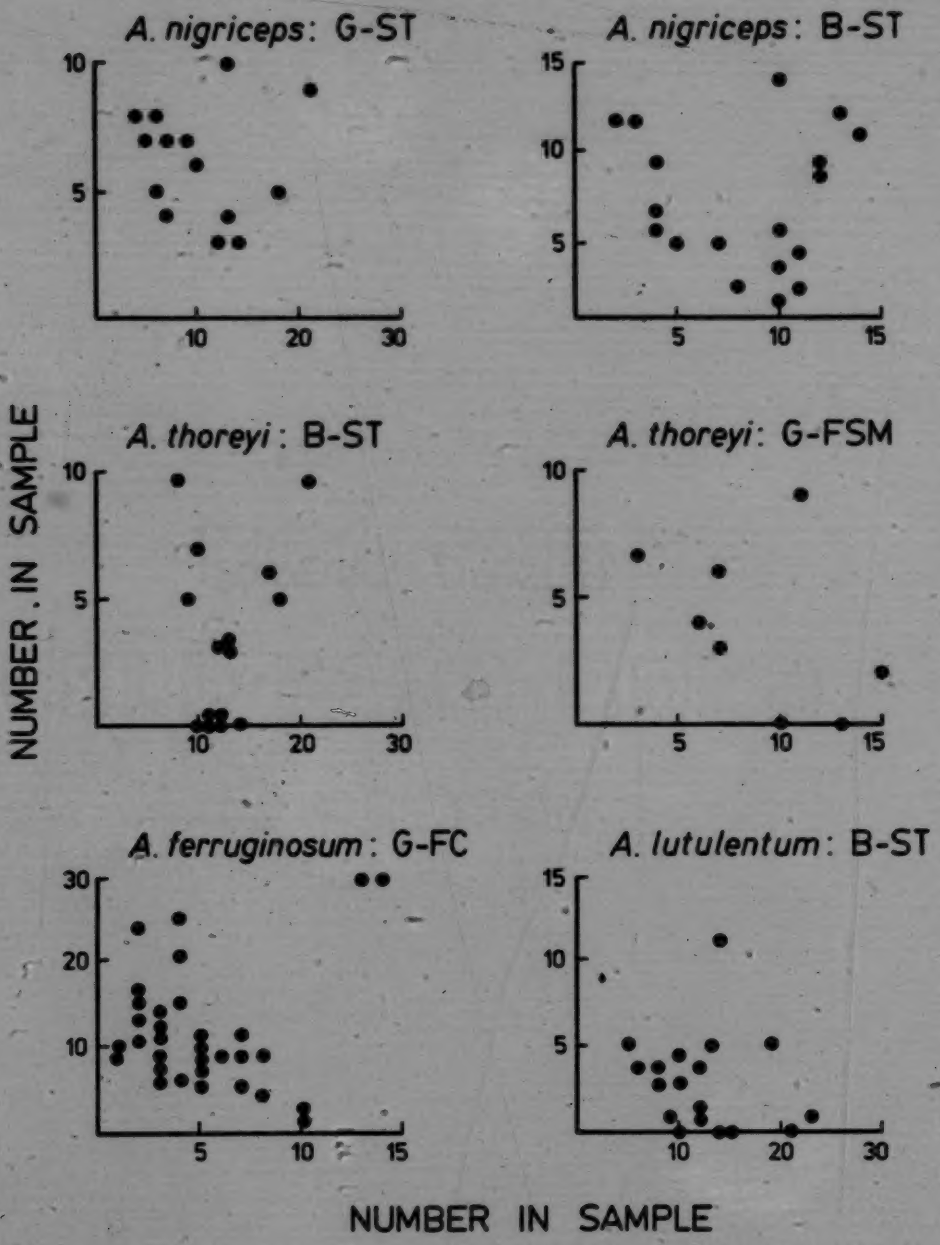
for George Lake, *A. nigriceps*, *A. ferruginosum*, *A. thoreyi*,

for Barrhead, the same as the preceding plus *A. lutulentum*.

Abbreviations are as follows:

G = George Lake; B = Barrhead; FSM = flooded sedge meadow;

ST = sedge tussocks; FC = floating cattails.


A. nigriceps: G-ST
A. nigriceps: B-ST
A. thoreyi: B-ST
A. thoreyi: G-FSM
A. ferruginosum: G-FC
A. lutulentum: B-ST
NUMBER IN SAMPLE
NUMBER IN SAMPLE
10
5
10
20
30
15
10
5
5
10
15
10
5
10
20
30
10
5
5
10
15
30
20
10
5
10
15
15
10
5
10
20
30

was that the abundance of a species in particular locations might have been affected not simply by the presence of just another particular species, but perhaps by the general level of crowding resulting from the combined abundances of all other species present.

Most correlations (Table 14) were negative, but only one coefficient, that for *A. nigriceps* in the George Lake cattails, reached significance level ($P<0.05$). The graphs of Figure 25 do not reveal any clearly polarized pattern of points as might be expected if marked, negative interactions existed among species. Negative values of the correlations might in part be due to the segregation of species along microhabitat dimensions, which was not taken into account in the analysis. The results therefore suggest that repulsive or negative effects cannot be detected among adults that co-occur in microlocations..

5.3.5 Size relationships

Table 15 provides body lengths and labrum widths of the four major guild members. With respect to body size, *A. nigriceps* is the smallest species of the group, *A. ferruginosum* and *A. lutulentum* are intermediate, not differing significantly, and *A. thoreyi* is the largest.

All four species significantly differ with respect to mouth size (indicated by labrum width), but again *A. nigriceps* and *A. thoreyi* have respectively the narrowest and the widest mouth. *A. lutulentum* has a narrower mouth than *A.*

TABLE 15

Body size and labrum widths
of co-occurring adults of marsh *Agonum*

A: BODY SIZES

SPECIES	N	BODY LENGTH (mm) MEAN	BODY LENGTH (mm) 95% C.I.
A. nigriceps	20	5.22	5.11 - 5.33
A. ferruginosum	21	5.99	5.88 - 6.09
A. thoreyi	20	6.76	6.66 - 6.87
A. lutulentum	18	5.87	5.76 - 5.98

B. LABRUM WIDTHS

SPECIES	N	LABRUM WIDTH (mm) MEAN	LABRUM WIDTH (mm) 95% C.I.
A. nigriceps	20	0.279	0.270 - 0.289
A. ferruginosum	21	0.337	0.328 - 0.345
A. thoreyi	20	0.367	0.356 - 0.378
A. lutulentum	18	0.312	0.304 - 0.319

ferruginosum, despite overlapping with it in body size. These data suggest that the species may differ in size of food items eaten.

Size relationships among species were further assessed by computing ratios of mean measures for species pairs. These results are presented in Table 16. The size gap is widest between *A. nigriceps* and *A. thoreyi*, reaching a value of 1.30. The gap between *A. ferruginosum* and *A. thoreyi* is narrower for mouth size than for body size, while it is the converse, albeit to a very slight degree, between *A. ferruginosum* and *A. lutulentum*. The data suggest that *A. ferruginosum* may overlap extensively with *A. lutulentum* relative to the small food items of its diet, and do so similarly with *A. thoreyi* relative to the large items of its diet.

TABLE 16

Body size and labrum width ratios for co-occurring adults of marsh *Agonum*

A. BODY SIZE RATIOS

	A. nigriceps	*A. ferruginosum*	*A. thoreyi*
A. ferruginosum	1.15		
A. thoreyi	1.30	1.13	
A. lutulentum	1.12	1.02	1.15

B. LABRUM WIDTH RATIOS

	A. nigriceps	*A. ferruginosum*	*A. thoreyi*
A. ferruginosum	1.20		
A. thoreyi	1.31	1.09	
A. lutulentum	1.16	1.08	1.18

5.4 Discussion

5.4.1 Macrohabitat overlap and diversity

High overlap values, particularly in the unflooded sedge meadow and wet forest floor, coupled with high species richness reveals a situation of tight species packing where keen competition would be predicted by niche theory (May and MacArthur, 1972; Pianka, 1974). Members of the forest margin guild occupy a structurally very simple habitat (leaf litter) and hence may find the potential for resource partitioning along spatial niche axes quite restricted. However the possibility that a range of undetected microhabitats are present at the forest margin cannot be denied; microsites probably are used by carabids, given their general selectivity for microenvironmental features and abiotic factors (Thiele, 1977: 172). Microsite partitioning would reduce significantly potential competitive interactions. Furthermore, average species densities were low at the edge of the marsh (compared with the flooded areas), hence the potential for competition may already be very reduced from that fact alone, assuming that resources are not highly limiting.

The above arguments indicate that the evidence for competition among carabids at the edge of the marsh appears weak in spite of the high degree of species packing (the flooded marsh guild will be dealt with in the following sections). It has been argued that failure to bring out good evidence for competition in many situations is because the observed patterns are postinteractive (MacArthur, 1972b: 132ff; Schoener, 1974). Likewise it might be said with respect to the species of the edge of the marsh that previous competition has resulted in populational adjustments to low densities by the widely overlapping members of the flooded zone guild to avoid severe competitive interference and resource depletion. The difficulty with a hypothesis of this sort is that the lack of historical evidence renders it untestable (Glass and Slade, 1980).

A most intriguing observation is the uniformity of the community in some macrohabitats in terms of relative abundance of species, as shown by very low variances in overall densities [an attempt was made to bring out this pattern using the Shannon-Weiner index H', but the variance exhibited by H' was so high (owing to too small sample size) that no differences among habitats emerged].

Relatively high uniformity of species composition of the Barrhead cattails could be due to the low abundance of *A. ferruginosum* and *A. thoreyi* apparently resulting from the lack of structural complexity of the habitat —both species markedly dominate the cattail guild at George Lake (see Chapter 2). Because of unsuitable structure, the Barrhead cattails may constitute only a transient habitat for epigaeic carabids; most species encountered may be dispersers "stopping over" temporarily, perhaps attracted in flight by the high profile of the cattail vegetation. A line of evidence supporting this idea is the actual finding in the cattails at both marshes of carabid species that are not at all marsh dwellers (e.g. long-winged individuals of *A. decentis* and *A. retractum*). Low populations of permanent residents plus several occasional dispersers, which may be mainly represented by unflooded zone species taking on short flights, could produce a relatively even faunal composition in that habitat.

In unflooded zone, especially the wet forest margin, habitat transience is less likely to explain low densities of all species, because virtually all of those encountered are genuine residents frequently found at the edge of flooded marshes. Relative uniformity in faunal composition thus seems somewhat at odds with the well known, widespread patterns of species abundances (May, 1975, 1976) following which communities usually include a few relatively common species, some intermediately common species, and a majority of rare species. It certainly seems unreasonable to hypothesize that the present situation could be produced by equal competitive abilities and/or comparable efficiencies of the species to exploit resources, merely because these parameters are functions of variables such as body size, reproductive effort and success, growth rate, and so on, which in all probability differ among species.

The most straightforward hypothesis for the near evenness of the faunal composition of the unflooded zone, especially of the forest margin, might involve extrinsic factors operating more or less equally upon all species considered. Environmental variability seems precluded, as again species-specific responses should be expected unless conditions were extreme or catastrophic, and they were not.

I suggest that the action of predators can likely explain the observed pattern. The preceding arguments notwithstanding, there are two lines of support in favour of this hypothesis. First, the impact of predators may be critically important in communities inhabiting structurally simple habitats with benign environmental conditions (Paine, 1966; MacArthur, 1972b: 30); the forest margin is a simple habitat and probably affords, on average, benign conditions. Second, there is incidental evidence that predators (esp. shrews) may account for much of the mortality in marsh carabids (Murdoch, 1966a), and there are reports that amphibians (common in and around marshes) eat indiscriminantly large numbers of carabids (Larochelle, 1974a, 1974b). Thus opportunistic insectivorous predators such as toads, frogs, and shrews, may exert significant impact on carabid populations of the relatively open litter of the forest margin. If prey selection is random, a common species will be picked more frequently than a rare one, and if predation efficiency is high, as it may be at the forest margin, action of predators may tend to equalize carabid populations of the various species in the community.

5.4.2 Breadth, overlap, and niche structure

The niche analysis presented in this chapter emphasizes that the species of marsh *Europhilus* constituting the guild in flooded marshes display different degrees of spreading over spatial and temporal niche axes, producing patterns of species segregation. Each species seems to be a specialist (narrow niche) over one resource set while being more or less a generalist over the other resource sets. This situation is predicted by conventional niche theory if resource partitioning results from high level interactions among species of the guild (Schoener, 1974).

Theoretical arguments (Levins, 1968: 44; McNaughton and Wolf, 1970) have predicted that broad-niche species or generalists should be numerically the most abundant in their environments because they are presumably better at exploiting a range of resources or states within resource sets. Field studies (e.g. Price, 1971; Longair, 1978) have indeed observed high abundances coincident with broad niche patterns. However other works found no relationship between the two parameters (e.g. Denno, 1980; Rotenberry and Wiens, 1980). The present investigation too did not reveal any clear relationship between high abundance and broad niche within the flooded marsh guild; rather the opposite pattern was observed (e.g. *A. nigriceps* with respect to microhabitats, *A. ferruginosum* with respect to macrohabitats). Significantly, Whittaker and Levins (1975: 178) cautioned against linking these two characteristics;

the relative magnitude of abundance and of niche breadth may, partly or wholly, depend on the geographical scale of the study and nature of niche dimensions considered.

Relative width or size of niches has been repeatedly connected with optimal foraging theory (Pianka, 1978: 256). A broad niche over one resource axis may thus reflect, for example, an optimal adaptation in an uncertain environment (Levins, 1968: 50). Such species adaptations might constitute a prime, though by no means the sole, determinant of niche size with respect to spatial dimensions for some marsh *Europhilus*. For example, lower foraging efficiency of *A. thoreyi* on vegetation, suggested by results of climbing experiments (Chapter 4), may explain its more restricted distribution over microhabitats of the flooded zone (dense patches of dead plants, emergent substrate), but the marked patchiness of suitable microsites may elicit a wide occupation of marsh macrohabitat zones. If so, microsite patches form a critical but uncertain (in space) variable in the habitat background of *A. thoreyi*. Analogous patterns have been observed in some tropical birds which could live in a variety of habitats provided these gave them opportunities for their specialties (Lovejoy, 1974, cited in Hutchinson, 1978: 171). Miller (1980) reported changing patterns of niche breadths in a guild of parasitic Hymenoptera that were seemingly related to temporal instability of habitats. Thus broad niches may be viewed as a form of spreading of the risk by populations of a species

(Boer, 1968), and not necessarily as a sign of dominance.

If the niche pattern of *A. ferruginosum* relative to habitat dimensions can be explained in ways roughly similar to that of *A. thoreyi*, that of *A. nigriceps* is different. The independence of adults of *A. nigriceps* over microhabitats defined by vegetation structure and their ability to climb lead to the prediction that the species should be more uniformly distributed throughout the flooded zone. Occurrence of population peaks in sedge tussocks thus implies that factors governing distribution of *A. nigriceps* over macrohabitats may differ from those affecting *A. ferruginosum* and *A. thoreyi*. Responses to undetected or unmeasured environmental variables are possible, but biotic interactions are certainly not precluded.

While niche breadth allows examination of a species distribution over resource axes independently of other guild members, analysis of niche overlap shows relationships among species relative to the resources concerned. Niche theory predicts that species overlapping extensively along a resource axis should diverge markedly along at least another axis if coexistence is to be permitted (Schoener, 1974; May, 1975; Pianka, 1975). Numerous studies have documented patterns of niche complementarity but few have demonstrated that it may result from competitive interactions (e.g. Werner, 1977) as theory predicts. Opposite patterns or niche convergence have even been found among coexisting bird species (Rotenberry and Wiens, 1980). In insects, Longair

(1978) observed that some niche complementarity in hole-nesting wasps was detectable but not clear. Likewise a blurred relationship among dimensions also seems to emerge from a study of salt marsh Homoptera by Denno (1980). The present study revealed that a pattern of complementarity existed among marsh *Europhilus* albeit to a moderate degree. Thus competitive interactions may possibly have affected the structure of the guild, but if so, their effects may have been mild or are perhaps obliterated by other factors, because complementarity seems weak. At any rate, if niche overlap is an indicator of actual or potential competition, it cannot be decided on that basis only in which pair of species such interactions may take place. The overall overlap index is greatest between *A. ferruginosum* and *A. thoreyi*, but this may be interpreted in two ways: either that competition will be keenest between these two species in the guild or, conversely, that low competition, or lack thereof, between them allows wide resource overlap. Such results and those of studies cited above suggest that properties of insect niches and their interrelations across coexisting species are not always explained adequately by present niche theory, emphasizing May's (1973: 6) remark about intertwining of resource dimensions.

5.4.3 Competition and size relationships

The correlation analysis of simultaneous abundances of *Europhilus* species at sample sites did not reveal any significant pattern of negatively related distributions and thus the data yielded no evidence that interspecific interactions might be affecting the species distributions on that fine scale. In fact, some samples had high numbers of one species correlated with high numbers of other species, suggesting that species may be brought together by similar responses to habitat or environmental features or habitat selection. However it should be borne in mind that the kind of interactions that the analysis attempted to detect was of a particular type, namely avoidance of crowding within microsites at precise times. Since competition or interspecific interactions of any type are dynamic, they are unlikely to be seen unambiguously by examination of random points in space and time, unless their action is pronounced and persistent. Hutchinson (1965: 61) and Wiens (1977) have argued that competition in nature, particularly in groups like insects, might be quite sporadic in space and time, and thus difficult to observe, except through experimental manipulations. Hence the present analysis does not support or refute the possibility of competition among adults. Laboratory observations (pers. obs.) of *Agonum* adults confined in containers indicate that they display little aggressiveness toward each other even when fairly crowded, providing that enough food is given. However when hungry, cannibalism and interspecific predation were observed. This suggests that if food becomes limited in nature, competition among adults is likely to take place.

Study of habitat use (Chapter 2) showed that distribution of *A. ferruginosum* and *A. lutulentum* were mutually exclusive when both species were present (Barrhead), but that *A. ferruginosum* occupied the peak macrohabitat of *A. lutulentum* when it was alone. Obviously this pattern could not have come through in the above correlation analysis because data from each macrohabitat were handled separately. However it suggests that if competitive displacement is involved, it may result in segregation over macrohabitats rather than microsites.

It has been proposed that allied species in competition could coexist if they differed in size (linear dimensions) by a factor of 1.2-1.3 (Hutchinson, 1959, 1965: 55), simply because this would allow differential exploitation of available food sizes. Analysis of body and mouth sizes indicated that several species pairs approximate this figure, especially in mouth size, though the values tend to be slightly lower than 1.2. Thus the size discrepancies among adults of most species suggest that competitive interactions may have occurred in the past, leading to character displacement in size, and hence diet differentiation. Similar observations have been made by Spence (1979a) for co-occurring *Nebria* species in which the size gap was most striking among larvae.

Interestingly, the figures would predict wide overlap in diet between *A. ferruginosum* and *A. lutulentum*, precisely those species which have an exclusive distribution pattern. The broad size overlap between them coupled with their spatial exclusion suggests that competitive displacement may be currently ongoing in the George Lake area, in marshes where both species co-occur in significant numbers. A historically recent contact in the area between the two species is not unlikely. Until quite recently, *A. lutulentum* was seemingly not reported from some parts of Alberta and a distributional gap in the Prairies had been hypothesized (Lindroth, 1966: 581). Sporadic occurrence of *A. lutulentum* in the study area, despite an abundance of presumably suitable habitats, also suggests a relatively recent invasion by this species.

Wilson (1975) has developed a model whereby predatory arthropods like carabids should not evolve conspicuous differences in body size for promoting niche partitioning. However that author noted that even though examples were not known, there was no *a priori* reason not to expect such size displacement patterns in small predatory arthropods. Hutchinson (1978: 175) mentions a possible case in backswimmers. Both Spence's (1979a) observations on *Nebria* and those of the present study in fact indicate that the pattern may be present in carabids. As Spence (1979a) pointed out, tests of character displacement hypotheses can easily be made by examining specimens from areas where the species are allopatric. Further work on the marsh *Europhilus* system should attempt to investigate size relationships among larvae, after they can be confidently identified, as it is this life stage at which interactions are likely to be more severe owing to the aggressiveness of larvae and to the fact that food resources are then critical for promoting growth.

6. GENERAL DISCUSSION

6.1 Resource partitioning among adult carabid populations

This study attempted to answer the broad question of how a set of co-occurring congeneric species of carabids inhabiting eutrophic marshes were distributed in space and time within that ecosystem. It established empirically that adult populations of the numerically dominant *Agonum* (*Europhilus*) species differed in spatial distribution within and between marshes at both the macro- and microhabitat level, and in aspects of population dynamics, notably those related to reproduction. A comparative summary of the principal natural history features of these species (Table 17) emphasizes these interspecific differences.

However the mechanisms underlying the observed niche divergences remain hypothetical. The question of whether and how coexistence in the guild would be imperiled if segregation in the use of capital resources was reduced or if ecologically severe conditions occurred (Wiens, 1977) will become meaningful only when those mechanisms are known.

The significant resource partitioning detected among adults of the species involved leads to the hypothesis that competition may have affected the structure of the guild since the time the species first met. Size similarities and seemingly mutual exclusion over habitats between *A. ferruginosum* and *A. lutulentum* even suggest that niche

TABLE 17

Summary of the main natural history features of the four dominant species of marsh *Agonum* in the George Lake study area, Alberta

FEATURES	*A. nigriceps*	*A. ferruginosum*
peak adult macrohabitat	sedge tussocks	cattails, but may vary with microhabitat features present
main adult microhabitat (flooded zone)	general	dense dead growth +dense tussocks
adult density in peak macrohabitat	up to 20 m^{-2}	up to 33 m^{-2}
beginning of breeding season	early spring just after thaw	early spring just after thaw
average fecundity	8 eggs/♀	16 eggs/♀
approx. duration of development (egg to adult)	4 months	3 months
probable larval macrohabitat	same as adults	same as adults
daily activity	nocturnal	nocturnal
relative body size	small	medium
position on R-K selection continuum	near K	near R

(continued on next page)

TABLE 17 (continued)

Summary of the main natural history features of the four dominant species of marsh *Agonum* in the George Lake study area, Alberta

FEATURES	*A. thoreyi*	*A. lutulentum*
peak adult macrohabitat	general, depends on microhabitat features present	sedge tussocks, but restricted in marshes occupied
main adult microhabitat (flooded zone)	dense dead growth +dense tussocks +emergent substrate	dense dead growth (?) +dense tussocks
adult density in peak macrohabitat	up to 12 m^{-2}	up to 10 m^{-2}
beginning of breeding season	late spring, 3-4 weeks later than other spp.	?
average fecundity	20 eggs/♀	?
approx. duration of development (egg to adult)	3 months	?
probable larval macrohabitat	same as adults	flooded sedge meadow (?)
daily activity	nocturnal	?
relative body size	large	medium
position on R-K selection continuum	near R	?

Question marks alone denote unknown information, while bracketed question marks denote uncertain information.

adjustments between these two species may not yet be complete owing to a relatively recent contact in the study region.

Marked resource division among *Agonum* adults contrasts with the results of Spence's (1979a) study of *Nebria*. In the latter, co-occurring adults showed insignificant segregation on any of the resources investigated (foraging time, microhabitat, food). Pronounced niche segregation was found in larvae however. A major difference between the *Nebria* guild and the *Agonum* guild is in abundance of adults. Spence noted that adult *Nebria* populations were at low densities and that their habitat was therefore probably unsaturated with adults. Adult populations of marsh *Agonum* are, in contrast, extremely dense, hence it is quite likely that niche differences have evolutionary roots, at least partially, in interspecific competition.

Possibly, resource partitioning in adult populations of sympatric carabids becomes increasingly important with increasing densities, while being relatively minor at low densities. Extent of niche separation might thus vary with the population characteristics of the group studied.

As regards marsh carabids, I proposed earlier (Chapter 2) that build-up of extremely high (for carabids) populations might be connected to both the high organic productivity of the marsh ecosystem and to exploitation of a habitat volume instead of a habitat surface. If environmental conditions become very harsh, for example, during a severe drought, the scramble for scarce resources, especially food, may quickly lead to pronounced competition among the dense populations of *Agonum*, and perhaps to exclusion or local extinction (within a marsh) of one or a few of the species.

During periods of favourable conditions (resource abundance) however, low aggressiveness of adults towards each other suggests little competition among them. Thus adult competition may be only intermittent, i.e. sporadic in space and time. On the other hand, one might expect interference competition among larvae to take place fairly frequently given both their high densities (at least as dense as adults) and their marked aggressiveness.

It remains to be demonstrated that in any field situation resources become severely limited for these marsh carabid populations and that this occurs frequently enough to both allow the evolution and reinforce the maintenance of niche differences among species. Density characteristics of flooded marsh populations certainly render this probable. Food is likely to be the key resource in competition owing to opportunistic feeding habits of these carabids. Both Murdoch (1966a) and Wasner (1979) obtained evidence suggesting that, indeed, food shortages with consequences on population size and fertility may periodically occur for marsh *Europhilus*.

6.2 Evolution and maintenance of niche differences

Ecological discrepancies within the species pairs are exhibited over different combinations of resource axes, the most pronounced ones involving separation in space. This multiplicity of patterns of niche differences is an indication that several processes, and not only competition, probably inter-play to produce and maintain the ecological separation of the species. It is even possible that the relative importance of each process differs for each species or pair of species, as this has been observed in other insect groups (e.g. gerrids, Spence, 1979b).

A. nigriceps is the most ecologically (spatially) isolated species of the guild mainly because of the independence of its distribution with respect to microhabitat features of the flooded zone in marshes. It seems to be the species best adapted to life on the emergent vegetation of marshes; the indicators of this are body coloration which confounds individuals with the habitat background, the highly developed climbing propensity related to the unique structure of the legs (tibiae shorter than tarsi), and perhaps also the K-selected characteristics (low fertility) reflecting low "risk" (*sensu* Boer, 1968) for the populations.

The cryptic coloration of *A. nigriceps* suggests that visually hunting predators (like frogs and birds) have had a significant impact on evolution of this species, possibly more than for the other carabid species of the inundated zone. It was hinted earlier (Chapter 5) that given its natural history characteristics, *A. nigriceps* should be more evenly distributed across marsh macrohabitats. Its marked peak in sedge tussocks may partly reflect lower predation pressures owing to the patchy nature of that macrohabitat and scattering of tussocks in open water pools. Over evolutionary time, lower predation in some parts of the marsh would contribute to enforce the habitat association or preference of that species.

There remains the question of why *A. nigriceps* might have been more susceptible to the action of predators in the course of its evolution than were the other species. Perhaps in the original populations, the ancestors or "*proto-nigriceps*" were at a competitive disadvantage (owing to small size) and were displaced from the parts of the flooded habitats most suitable to epigaeic carabids (e.g. dense patches of dead plants, emergent substrate). Occurrence on more open vegetation could in turn have rapidly led to the evolution of traits such as cryptic coloration and climbing.

Sensitivity of the distribution of *A. ferruginosum*, *A. thoreyi* and *A. lutulentum* adults to microhabitat features and their lower propensity to climb suggest that structure of the habitat background may be an important variable in the interrelations of their niches. Comparison of the George Lake and Barrhead sites provides insights as to how the presence or absence of certain microsites may alter distribution and abundance of these species within inundated macrohabitats. In that context, habitats and their variation, especially in space, provide the "template" (Southwood, 1977) which evokes population responses from the species and thus governs coexistence patterns.

A. ferruginosum appears to be the species able to build the largest populations in the field, as reflected by the extremely high density it reached in the George Lake cattails. This species might gain advantages from commencing reproductive activity very early in the spring and from a high fertility and an apparently fast growth indicated by tenerals already emerging in early July. It benefits from an absolute size advantage over *A. nigriceps*, which starts reproducing at the same time, while early breeding may grant it with a relative size advantage over the bigger, but later breeding *A. thoreyi*. This scheme suggests two possible ecological adaptations accounting for the success of *A. ferruginosum* in the cattails: either it is competitively superior and pre-empts the most favourable macrohabitat (with dense vegetation), or it is an opportunistic species with a potential to build large populations when habitat conditions are optimal. Its lower density at Barrhead and particularly its apparent exclusion from sedge tussocks in presence of *A. lutulentum* give support to the second alternative.

A. thoreyi exhibited the highest fertility but on average had lower densities than either *A. ferruginosum* or

A. nigriceps. This suggests that mortality may be high in the immature stages of this species. Interspecific interactions may likely play a role in causing part of the mortality perhaps owing to a size disadvantage in the early larval instars. This disadvantage might preclude *A. thoreyi* from achieving pronounced population peaks in any part of the marsh. Thus the generality of the distribution of *A. thoreyi* over macrohabitats may to some extent result from its delayed reproductive period relative to that of the other species. Other factors might involve ability to find or select patchy suitable sites. If *A. thoreyi* possesses this capacity to a lesser degree than the other species of the flooded marsh, it may not be able to achieve comparable population performances.

Annual migration of individuals out of the marsh for overwintering (Dawson, 1965; Murdoch, 1966a) implies that proper habitat selection by the species should operate at the time of spring colonization of the different marsh macrohabitats. Finding areas of a marsh affording optimal vegetation structure for efficient foraging might guarantee successful reproduction and high population performance. Species-specific adaptations and responses to habitat structure might thus have been a central theme in the evolution of niche relationships among *Europhilus* species dwelling in inundated marshes. Spence (1979b) found this for a guild of coexisting gerrids in which niche boundaries were seemingly tested yearly. For these gerrids, habitat selection in the spring was the primary factor, but its effects could be altered by a combination of other factors including differential susceptibility to predation losses and to water surface disturbances, differences in growth rate, competition and local microclimate. It is therefore reasonable to expect a similar combination of processes to operate on the annual time scale on the *Europhilus* populations of each marsh. Given such conditions, and adding the variability of weather regimes that drive population growth and affect the availibility of resources such as food, it is likely that populations of marsh *Europhilus* are seldom in an equilibrium state.

6.3 Concluding remarks

This work lays a foundation for studying the various mechanisms that affect population responses and produce the observed niche patterns in marsh *Agonum* (*Europhilus*). The hypotheses and questions that were generated through interaction with theory should help single out significant ecological variables and design experiments needed to unveil the processes operating on the marsh *Europhilus* guild.

Experiments might well begin by testing effects of habitat structure on the species distribution and by investigating extent of habitat selection. Through comparisons of two marshes, this study also provides a launching pad for further field work that could cover a range of marshes within a small geographical region and examine how habitat variations affect the species composition of individual marshes and their abundances. Solving problems of larval sampling will undoubtedly be a crucial point because this would entail meaningful comparisons of population dynamics at the life stage that may be the most important one for ultimately determining relative success of species populations.

Even though the scheme of ecological relationships discussed above is largely conjectural, it stresses the fact that single-factor explanations will not capture realistically causes underlying observed niche differences. The empirical data of this endeavor suggest a blend of both biotic and environmental effects on populations of marsh *Europhilus* and also on other carabids of the community dwelling at the marsh edges. In this respect, they support the remark made in the general introduction to the effect that coexistence in carabid guilds certainly revolves around more than solely species-specific responses to abiotic factors. The results thus emphasize Hutchinson's (1975) point that meaningful progress in understanding ecological relationships will only emerge from first acquiring a thorough knowledge of the details of the natural history of the species involved.

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APPENDIX I

LIST OF MARSHES STUDIED DURING 1979 AND 1980 FIELD SEASONS

MARSH NO.	MARSH NAME[1]	DENSITY AND HABITAT SAMPLING	FEMALES COLLECTED FOR OVARIES[2]	*A. nigriceps* WING DIMORPHISM COLLECTING
1	Lake 1*	1979 + 1980		X[3]
2	Lake 2*	1979 + 1980		X[3]
3	Lake 4*	1979		
4	Lake 5*	1979	X	
5	Lake 6*		X	
6	Lake 7*		X	
7	Field 1	1979	X	X
8	Field 2	1979	X	X
9	Field 3	1979		
10	Field 4		X	
11	Road South 1			X
12	Road South Big			X
13	Busby	1979		X
14	East Alexander			X
15	West Morinville			X
16	Barrhead	1980		X
17	Barrhead Yoder		X	X
18	Nakamun 1			X
19	La Nonne 1			X
20	La Nonne 2			X

[1] All marsh names are unofficial.

[2] During 1980 field season.

[3] Results pooled.

* Marshes named "Lake x" are on the edges of George Lake.

APPENDIX II

ONE-WAY ANALYSES OF VARIANCE
FOR THE EFFECT OF MACROHABITAT CATEGORIES
ON OBSERVED DENSITIES OF *AGONUM*
AT TWO MARSHES

A. GEORGE LAKE

SOURCE	df	S.S.	M.S.	F	p
A. nigriceps					
between habitats	4	65.73	16.43	52.71	<.001
within habitat	218	67.97	0.31		
A. ferruginosum					
between habitats	4	103.21	25.80	58.56	<.001
within habitat	218	96.05	0.44		
A. thoreyi					
between habitats	4	17.66	4.42	9.66	<.001
within habitat	218	99.65	0.46		

Variances are heterogeneous in all tests (Bartlett's test: $p<.01$).

B. BARRHEAD

SOURCE	df	S.S.	M.S.	F	p
A. nigriceps					
between habitats	3	39.59	13.20	40.01	<.001
within habitat	177	58.37	0.33		
A. ferruginosum					
between habitats	3	30.98	10.33	35.72	<.001
within habitat	177	51.17	0.29		
A. thoreyi					
between habitats	3	14.02	4.67	10.27	<.001
within habitat	177	80.56	0.46		
A. lutulentum					
between habitats	3	12.63	4.21	20.36	<.001
within habitat	177	36.61	0.21		

Variances are heterogeneous in all tests (Bartlett's test: $p<.01$).

APPENDIX III

F-RATIOS AND THEIR PROBABILITY
(FROM ONE-WAY ANALYSIS OF VARIANCE)
FOR THE DIFFERENCE IN DENSITIES OF *AGONUM* SPECIES
IN VARIOUS MICROHABITAT CATEGORIES

SPECIES	F	p	HOMOGENEITY OF VARIANCE*
SEDGE DEAD GROWTH -1979			
A. nigriceps	2.10	.149	yes
A. ferruginosum	72.11	<.001	no
A. thoreyi	82.69	<.001	no
SEDGE DEAD GROWTH - 1980			
A. nigriceps	2.06	.158	yes
A. ferruginosum	32.97	<.001	no
A. thoreyi	84.21	<.001	no
CATTAIL DEAD GROWTH - 1979			
A. nigriceps	0.14	.705	yes
A. ferruginosum	9.99	.002	yes
A. thoreyi	6.82	.011	yes
CATTAIL EMERGENT SUBSTRATE - 1979			
A. nigriceps	2.63	.110	yes
A. ferruginosum	0.82	.368	yes
A. thoreyi	9.66	.003	yes
TYPE OF SEDGE TUSSOCK - 1980			
A. nigriceps	0.37	.547	yes
A. ferruginosum	9.52	.006	yes
A. thoreyi	14.89	<.001	yes
A. lutulentum	5.59	.024	---

* Bartlett's test

APPENDIX IV

INCUBATOR CONDITIONS AND SCHEDULES OF THE CLIMBING EXPERIMENTS

A. INCUBATOR CONDITIONS

EXPERIMENT	PHOTO-PERIOD (L:D)	TEMPERATURE (°C)	TYPE OF LIGHTING	DAY-LIGHT INTENSITY (Lux)
1 (1978)	16:8	17 ± 2	2 fluorescent tubes	50
2 (1979)	15:9	15 ± 2	2 100-watt incandescent bulbs dimmed by opaque glass	20-40[2]
2a (1979)[1]	14:10	17 ± 2	1 fluorescent tube	15-20[2]
3 (1980)	13:11	22 ± 2	2 7.5-watt incandescent bulbs	5-10[2]

[1] *A. cupreum* was tested at a later date because specimens could not be found in the field at the time experiment 2 began.

[2] Minimum and maximum values are provided, as intensity varied according to location into incubator.

B. SCHEDULES

EXPERIMENT	SETTING DATE	RECORDING DATES	
		START	END
1 (1978)	July 15	July 18	Aug. 21
2 (1979)	Aug. 3	Aug. 7	Aug. 15
2a (1979)[1]	Sept. 9	Sept. 17	Sept. 24
3 (1980)	Sept. 10	Sept. 19	Sept. 27

[1] *A. cupreum* was tested at a later date because specimens could not be found in the field at the time experiment 2 began.

AUTOBIOGRAPHY

I was born on May 14, 1955 in Lévis, Québec. Our family lived in Québec City until 1959, then moved to Lévis, where I completed my primary schooling. In 1968, I entered the Collège de Lévis for my secondary education. Among the first classes I attended were lectures in the natural sciences, especially botany and geology, in which I became at once keenly interested. Noticing my interest as I brought him various plants and mushrooms, my professor, Father Jacques Beaudoin, invited me to join the Collège's natural science club. There, during week-ends, I began to study botany, ornithology and limnology. In June 1969, I went to Father Beaudoin's science camp at St-Nérée, south of Québec City, where I was supposed to study limnology in the field for a few days. However, the view of brightly colored damselflies and beetles around the camp and in collection boxes drew my instantaneous fascination. I immediately quit limnology for entomology and, that summer, I seriously began collecting insects, especially beetles.

I remained a member of the science club for the seven years I spent at the Collège de Lévis, actively collecting and studying beetles. During the summers of 1970 to 1972, I attended intensive study periods in entomology at natural science camps in Québec. During the summers of 1973 to 1975, I worked as an entomology instructor at the Camp des Jeunes Ecologistes at St-Nérée, and in 1975, was also responsible for coordinating the scientific programme of that camp. That year, I also joined the Conseil de la Jeunesse Scientifique (CJS) of Québec as a member of the board of trustees, and later, became a member of its executive board. Through this benevolous activity, I took part in the coordination of scientific activities for the youth of the province, such as science fairs, clubs and camps. In 1976, I took the part-time job of regional director of the CJS for the Québec City area, which helped me earn some money while keeping me in touch with the scientific activities of the youth.

I became a member of the Association des Entomologistes Amateurs du Québec (AEAQ) in 1974 and this widened my contacts with other amateur entomologists and insect collectors. I was vice-president of the AEAQ in 1976, and its treasurer in 1977.

I was admitted to Université Laval in Québec City in 1975 in a three year B.Sc. programme in Biology. Summer jobs included working for Dr. J.M. McLeod of Environment Canada at Lac Normand, Québec in 1976 on a project on the Swaine Jack Pine Sawfly, and for both Dr. L. Jobin of Environment Canada and Dr. J.M. Perron of Université Laval at Anticosti Island in 1977 on Hemlock Looper outbreaks. Courses, term reports and discussions with professors at Laval, as well as summer jobs, directed my interests in a systematic and ecological direction.

Throughout these years, I kept collecting beetles, and my interest focused on carabids. My interest in the carabid fauna of marshes arose through a series of collecting trips in southwestern Québec in 1976-1977, during which I was impressed with the abundance of carabids in cattail marshes and by the fact that so-called "ground-beetles" lived among inundated vegetation. Realizing that little work had been done on the ecology of marsh carabids, I decided to make this the subject of my Masters research.

Advice and encouragement from Henri Goulet, a former Ph.D. candidate of this Department, and an evening discussion over beer with Dr. George E. Ball at Laval in 1977 convinced me to attend the University of Alberta. Upon completion of my B.Sc. at Laval, I moved to Edmonton in May 1978 to undertake a Masters programme, the results of which are reported herein. In June 1979, I married Marie Dumas in Montréal.